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Joyce Allan, F.R.Z.S.

Miss Allan, Patron of the Society since 1956, is a recognized authority on mollusca; was the well-known Curator of Shells at the Australian Museum, Sydney, until 1956. She is the author of a great number of specialized conchological papers, including those in the *Australian Encyclopedia* (1958). Miss Allan is also known as the author of *Australian Shells*, *Cowry Shells of World Seas*, and recently, joint author with Gilbert Whitley in *The Sea Horse and Its Relatives*. She attended the International Congress of Zoology held in Copenhagen as Australian Representative, and also that of the Nomenclature Council. Miss Allan was the first woman to be given an F.R.Z.S. for her services to science.

R. Tucker Abbott, Ph.D.

Patron of the Society for the past two years. Professor Abbott occupies the Pilsbry Chair of Malacology established in 1954 at the Academy of Natural Sciences in Philadelphia. His book on *American Sea-shells*, published in 1954, was followed by a smaller work in 1955, *Introducing Sea-shells*. He is a co-editor of the periodical *Nautilus*, and is editor-in-chief of *Indo-Pacific Mollusca*, a new series of taxonomic monographs of the marine mollusca of the Indo-Pacific which has just commenced publication.





Bernard Charles Cotton, F.R.Z.S.

Patron of the Society since 1956. Mr. Cotton is Curator of Molluscs at the South Australian Museum, Adelaide; past President of the Royal Society of South Australia; editor *South Australian Naturalist* for seventeen years. He is also author of *British Science Guild Handbooks* on South Australian Mollusca; Foundation Honorary Member of the Malacological Section of the Royal Society of South Australia, and Consulting Malacologist to the Natural Science Foundation, Philadelphia. Mr. Cotton was awarded the Australian Natural History Medallion in 1950. His newest publication, *South Australian Mollusca Archaeogastropoda*, came out in July, 1959.

OBITUARY

CHARLES FRANCIS LASERON

Mr. Charles Laseron, who died in Sydney on 27th June, 1959, has during recent years made many notable contributions to Australian malacology. His early life was a most varied one, and included a trip to the Antarctic with Mawson's 1911-1914 expedition, many years of work as collector for the Technological Museum in Sydney, and service in two world wars, including the Gallipoli landing, as well as an intense interest in collecting shells.

Towards the close of his working life, he took up the scientific study of the marine molluscs in his collection, and soon found an enormous field for original research on the minute species which had been largely neglected by earlier workers. Starting with the New South Wales Marginellidae and Rissoidae in 1948 and 1950, he worked group by group through the smaller shells, later on expanding his studies to the Queensland and Northern Australian forms. His papers were always illustrated with his own drawings, which at first were simple, though adequate, and later reached an excellence which has seldom been equalled for small molluscs.

Some workers might not have agreed entirely with his systematics, but none would doubt the intense and absorbing interest which he found in these tiny shells and the endless hours of patient observation which went into the sorting, description and drawing of the many species with which he dealt. Laseron's work will stand for years as a basic reference for all who seek to identify the minute mollusca of eastern Australia.

Donald F. McMichael, Ph.D., Curator of Molluscs,
The Australian Museum.

TWO NEW GENERA OF LAND MOLLUSCS (PAPUININAE) FROM THE CENTRAL HIGHLANDS OF NEW GUINEA

By W. J. CLENCH, Ph.D.,* and R. D. TURNER, Ph.D.†
(Plate 1, Text fig. 1-3.)

We are grateful to Dr. D. F. McMichael of the Australian Museum, Sydney, for specimens of the species described below, one of which is new. Both species were obtained near the head of the Wahgi Valley, not far from the base of Mt. Hagen. These were collected in 1946 by F. S. Mayer. Dr. E. O. Wilson of the Biological Laboratories, Harvard University, collected *Papuanella ogeramuensis* (Kobelt) and *P. finisterrensis* (Kobelt) during his trip to the Huon Peninsula in 1955.

WAHGIA gen. nov.

Shells depressed, trochoid in shape with the body whorl descending rapidly to form the aperture which is directed downward but not constricted. Aperture sub-elliptical with the peripheral area extended to form a "beak" and having a slight indication of a papuinoid notch. Whorls carinate.

In the reproductive system, the spermatheca is globular and has a very short spermathecal duct. The penis is short and has a small epiphallus with the vas deferens coming from the side and the penial retractor muscle attached to the penis at the base of the epiphallus.

Type species, *Wahgia juliae* Clench and Turner.

WAHGIA JULIÆ sp. nov.

(Plate 1, fig. 1-3; text fig. 1; text fig. 2, fig. 2-3.)

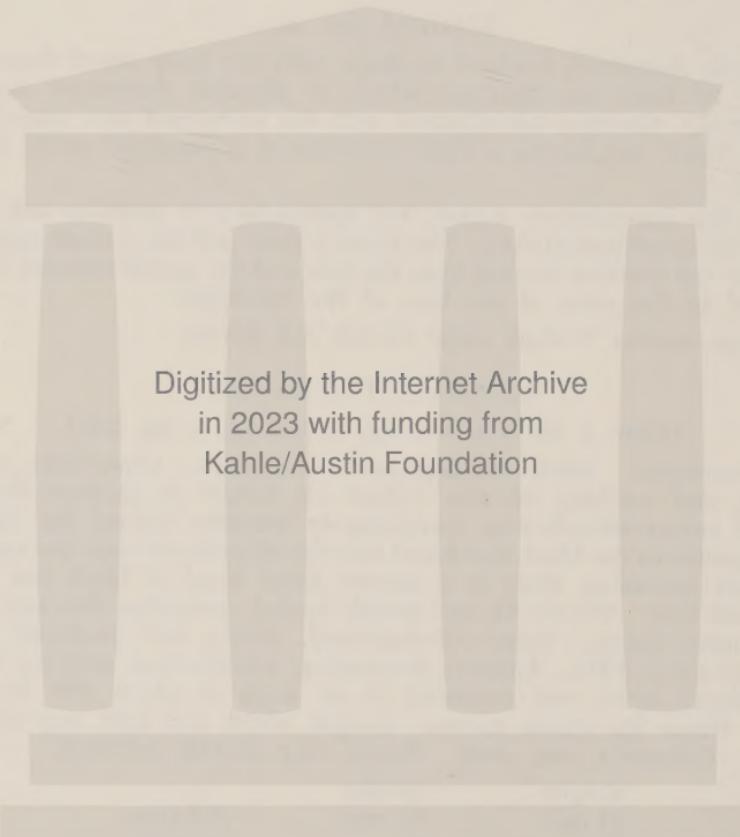
Description. Shell sub-depressed, trochiform, imperforate, nearly smooth, and reaching 34 mm. (about 1½ inches) in greatest diameter. Ground colour olive-brown, increasing in intensity toward the lip. On some specimens the black is diffused into the olive-brown near the aperture. On most specimens there is a narrow spiral band of black just above the acute keel. Whorls 4½ and acutely keeled, somewhat flattened above and convex below. Spire sub-depressed, obtuse and produced at an angle of about 100°. Aperture descending, sub-elliptical, rostrate, with a well-defined notch and produced at an angle of about 25° from the base. Outer lip rather narrow, straight above the keel and reflected below. Columella very short. Suture very slightly indented.

Height	Width	
21 mm.	32 mm.	Holotype
20.5	33	Paratype
21.5	34.5	Paratype
18.5	27.5	Paratype
18	28	Paratype

Types. The holotype of *Wahgia juliae* is in the Australian Museum, Sydney, Australia, no. C.62212. The type locality is twelve miles N.E. of Mount Hagen Range, Sepik-Wahgi Divide, New Guinea, at 5000-6000 feet, F. S. Mayer collector, November 1946. Paratypes from the same

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locality are in the Australian Museum no. C.62213 and the Museum of Comparative Zoology no. 191399 and 191400.

Remarks. This is a very distinctive species and we know of nothing to which it is closely related. It appears to be nearest in both shell morphology and type of colouration to *Pompalabia macgillivrayi* (Forbes) of northern Queensland, but the reproductive systems are quite different. The spermatheca in *juliae* is globular with a very short spermathecal duct, while in *macgillivrayi* the spermatheca is oval and the stalk is sixteen times as long as the spermatheca. The penial apparatus in *juliae* is short and is without a flagellum; in *macgillivrayi* it is long and has a flagellum. This new species has a superficial resemblance to *Rhynchotrochus*, differing mainly in its type of colouration but again very different in its soft anatomy. The penis of *Rhynchotrochus tayloriana* (Adams and Reeve) is elongate and has a long, narrow epiphallus with the vas deferens and a small flagellum at the end. In *juliae*, the epiphallus is very short and thickened, with the vas deferens coming from the side, and no flagellum.

Specimens examined. NEW GUINEA: Twelve miles north-east of Mt. Hagen, Sepik-Wahgi Divide at 5000-6000 feet; hills south of Baiyer River, about 20 miles north of Mt. Hagen (AM; MCZ).

PAPUANELLA gen. nov.

Shells trochoid in shape with the body whorl of the adult descending slightly to form the aperture which is directed downward and is somewhat contracted. Aperture subcircular to ovate. The lip is simple, slightly thickened but not reflected, and lacking a papuinoid notch. Whorls convex and slightly carinate.

The reproductive anatomy is characterized by a ovate spermatheca with a moderately long spermathecal duct. The penial apparatus is short and has a moderately thick wall with a short and recurved epiphallus. The penial retractor muscle is attached to the epiphallus at the recurved area. In general shell outline this genus is shaped similarly to *Noctepuna* of Queensland, but the reproductive systems of these two groups are very different, and in shell characters they differ in that the aperture of *Noctepuna* is not constricted.

Type species, *Geotrochus ogeramuensis* Kobelt.

PAPUANELLA OGERAMUENSIS (Kobelt).

(Plate 1, fig. 4-7, text fig 2, fig. 1, 4; text fig. 3.)

Geotrochus ogeramuensis Kobelt 1914, *Nachrichtsblatt Malak. Gesell.* 46, p. 5; *ibid* 1917, 49, p. 5, pl. 1, fig. 4. (Ogeramua [Finisterre Mts.] German New Guinea).

Description. Shell extended, trochiform, imperforate, nearly smooth, glossy and reaching 25 mm. (about 1 inch) in greatest diameter. Ground colour yellowish to light yellowish green with a few specimens being a reddish brown. Occasional specimens may be a uniform greenish yellow, though there is generally one, and sometimes up to five, spiral bands of colour which range from brown to nearly black. The body whorl is usually predominantly green. Earliest 2½ whorls dark brown to black. The umbilical area and the inner surface of the lip black to bluish black. Interior of the aperture bluish black. Whorls 5 and moderately

convex with the periphery of the body whorl faintly keeled. Spire extended, acute and produced at an angle of about 65° . Aperture subcircular to ovate, slightly descending and cast at an angle of about 27° from the base. Outer lip simple, straight and without a papuinoid notch. Parital wall thinly glazed. Columella short, slightly curved and dark brown edged with gray. Sculpture consisting of very numerous and fine diagonal growth lines, nuclear whorls smooth.

Height	Width	
24.5 mm.	25.5 mm.	15 miles N.E. of Mt. Hagen.
23	24	15 miles N.E. of Mt. Hagen.
21.5	22	15 miles N.E. of Mt. Hagen.
21	20.2	15 miles N.E. of Mt. Hagen.

Types. According to Sherborn (1940) the Kobelt collection is in the museum at Frankfurt a/M. The type locality is Ogeramuua, Finisterre Mountains, German New Guinea.

Remarks. This is a very variable species, particularly in colour, ranging as it does from a uniform light greenish yellow to specimens which are nearly uniform dark blackish brown. The dominant colour pattern, however, is a yellowish green with a peripheral band of blackish brown.

The reproductive system of *P. ogeramuensis* is characterized by its short, thick-walled penis which has a short, recurved epiphallus with the vas deferens coming from the side near the end. The spermatheca is ovate and the spermathecal duct is about one-third the length of the uterus. *Papuanella finisterrensis* (Kobelt) has a very similar reproductive system.

Range: The range of the species, so far as now known, extends from Telefomin, east-south-east to the Huon Peninsula, a distance of about 450 miles.

Specimens examined: NEW GUINEA: Aiyura, 80 mi. N.W. of Lae at 6000 ft.; Minj, 55 mi. W. of Goroka; 15 mi. N.E. of Mt. Hagen Range at the Sepik-Wahgi Divide at 5000-6000 ft.; hills south of Baiyer River about 20 mi. N. of Mount Hagen; 2 mi. S. of Telefomin, Victor Emanuel Range (all AM; MCZ); Gemeheng, Hube area and Tumnang, Mangi Watershed, both Huon Peninsula (both MCZ).

PLATE I.

Fig. 1-3, *Wahlia juliae* Clench and Turner, 12 mi. N.E. of Mt. Hagen, Sepik-Wahgi Divide, New Guinea. Fig 1. Holotype, Australian Museum no. C.62212.

Fig. 2. Paratype, Museum of Comparative Zoology no. 191399.

Fig. 3, Paratype, Museum of Comparative Zoology no. 191400 (all 1.6x).

Fig. 4-7. *Papuanella ogeramuensis* (Kobelt), 15 mi. N.E. of Mt. Hagen, Sepik-Wahgi Divide, New Guinea.

Fig. 4-6. Australian Museum no. C.62214.

Fig. 7. Museum of Comparative Zoology no. 191399 (all 2x).

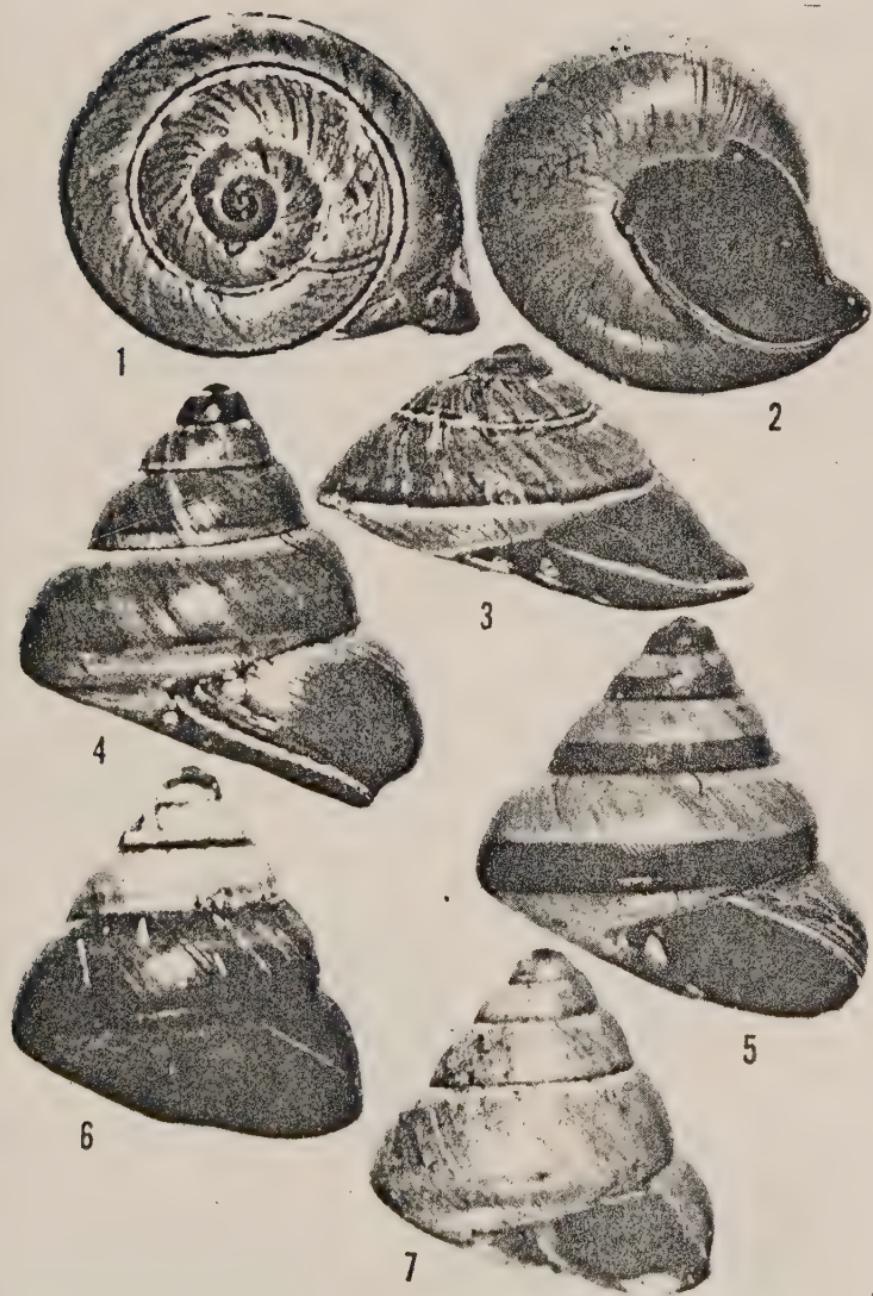
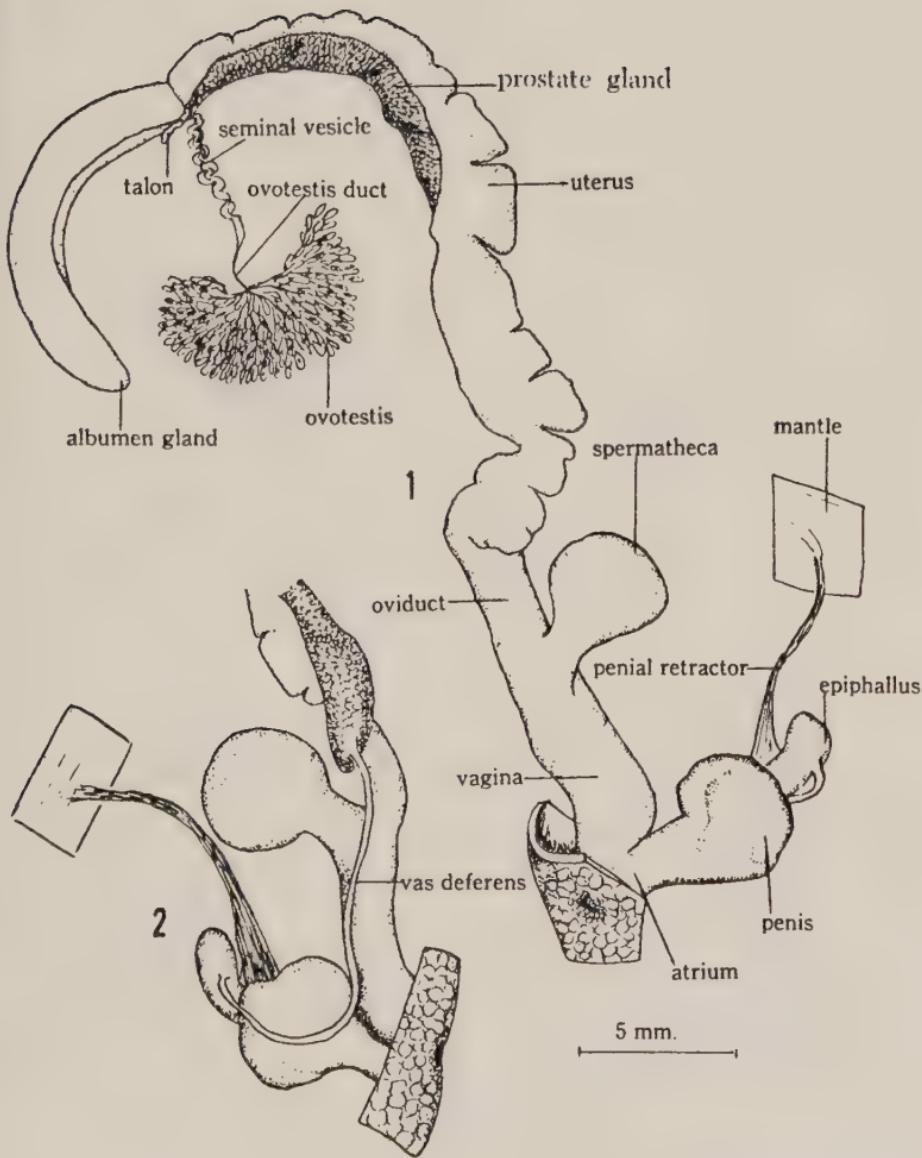


PLATE I.

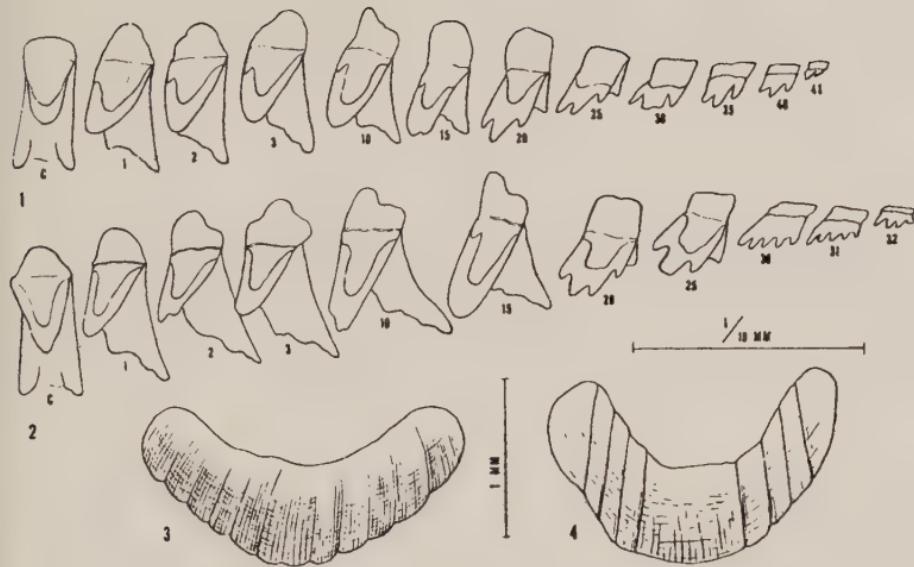


Text fig. 1.

Reproductive anatomy of *Wahgia juliae* Clench and Turner.

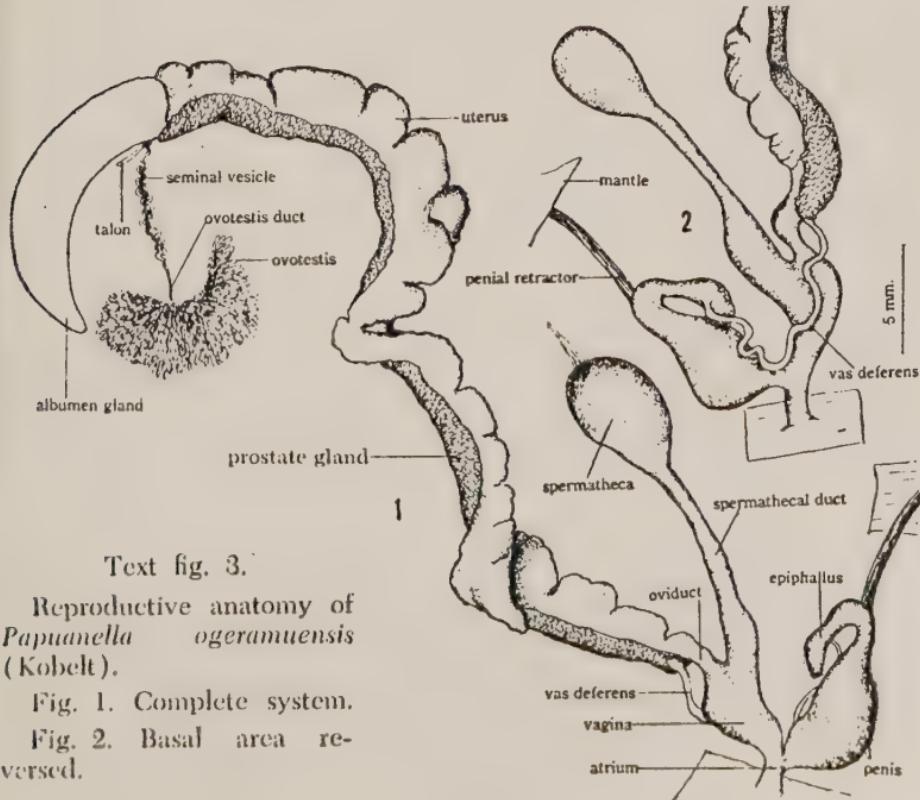
Fig. 1. Complete system.

Fig. 2. Basal area reversed.



Text fig. 2.

Fig. 1. Radula of *Papuanella ogeramuensis* (Kobelt).
 Fig. 2. Radula of *Wahgia juliae* Clench and Turner.
 Fig. 3. Jaw of *Wahgia juliae* Clench and Turner.
 Fig. 4. Jaw of *Papuanella ogeramuensis* (Kobelt).



Text fig. 3.

Reproductive anatomy of
Papuanella ogeramuensis
 (Kobelt).

Fig. 1. Complete system.
 Fig. 2. Basal area re-
 versed.

CHANGES IN SHAPE WITH TIME IN AUSTRALIAN SPECIES OF AUCELLINA POMPECKJ (AVICULOPECTINIDAE)

By RUDOLF O. BRUNNSCHWEILER, Ph.D.*

(Text Fig. 1-7.)

ABSTRACT.

Progressive changes in shape and size with time of right valves of a series of forms of *Aucellina Pompeckj*, the best known of which is *Aucellina hughendenensis* (Etheridge sen.), are demonstrated. The presumably genetically controlled variations took place during upper Albian times, i.e., during the time of deposition of what is known as the Tambo Formation of the Great Australian Artesian Basin. Systematic position and phylogeny of *Aucellininae nov.* are discussed.

INTRODUCTION.

The individual elements of the marine faunas contained in the Lower and Middle Cretaceous formations of the Great Australian Artesian Basin are fairly well known from numerous publications by pioneers of Australian Mesozoic palaeontology such as W. B. Clarke, R. Etheridge sen., R. Etheridge jun., W. H. Hudleston, F. McCoy, C. Moore, J. E. T. Woods, F. W. Whitehouse, and some others. A very important aspect of the biostratigraphy of the eastern Australian Cretaceous, however, is still in its infancy. It is the establishment and delimitation of local faunizones, their correlation with each other, and their relation with standard zones overseas.

The first serious attempt to subdivide the Cretaceous System of the Artesian Basin according to faunizone concepts was made by Whitehouse (1926a, 1926b, 1927, 1928). Through an admirable analysis of all then known ammonites he established which of the standard zones of the Aptian and Albian Stages are likely to be represented in the Artesian Basin formations provided always, of course, that the succession of species responsible for the European standard time-scale can be assumed to repeat itself in the form of more or less closely related, analogous, form series in Australia.

Broadly speaking, the assumption of such repetition is part of the fundamental working hypothesis applied to palaeontological-stratigraphical correlation problems. However, the early and rather uncritical enthusiasm for this hypothesis has in the last two or three decades been somewhat damped. While it still holds good in principle, it has also become evident that the concept had been driven too far when it was assumed that any, even the smallest, subdivision of a faunizonal time-scale was a world-wide recognizable thing.

Whitehouse (*loci cit.*) was working under a significant handicap. Although he described and analysed a great number of ammonites from various collections, he had little or no exact information on and could therefore not vouch for their relative position within the formations whence they came from. He was able to show, e.g., that genera and species, which, in Europe, are found together in a certain zone, have

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their phenotypical counterparts in a formation of the Artesian Basin sequence. Yet there does not *eo ipso* follow that the Australian forms are contemporaneous in the same way as are their European cousins. In the absence of direct field evidence Whitehouse simply had to assume that this is so. This may well be correct, of course, but to this date Whitehouse's zonal subdivision of the eastern Australian Cretaceous has not been factually substantiated and remains a working hypothesis the applicability of which must still be demonstrated.

This paper is a small step in a similar, or parallel, direction. By the example of *Aucellina* is shown what interesting results may be obtained from the study of faunas encountered in continuous bore cores. Thousands of bores have, of course, been drilled in the Artesian Basin in order to tap the vast water resources it contains. Unfortunately, the great majority of these bores were sunk with percussion (cable) tools. There are consequently scarcely any worthwhile records of macrofossils in the respective logs. Even from the limited number of bores in which cores were taken one knows preciously little about the sequence of fossils in the formations that have been penetrated.

The continuously cored bore which yielded the hereafter described series of *Aucellina* forms was drilled in 1957 by an oil company a few miles north-west of Oodnadatta, in northern South Australia, i.e., in the western marginal region of the Great Artesian Basin. To my knowledge it is the first continuous bore section whose succession of marine Cretaceous faunas has been recorded in detail while drilling was in progress. Not unexpectedly, I found a number of characteristic genera and species to be restricted to certain levels within the formations, but this short paper is not the place in which to enlarge on these interesting and important observations which have opened promising new avenues for more accurate and useful local zoning of the Cretaceous System in Eastern Australia.

For the present state of our knowledge on the stratigraphy and structure of the Great Artesian Basin the reader is referred to the up-to-date summaries by Sprigg (1958), Sprigg and Staff (1958), Whitehouse (1954), and David ('950). In Sprigg and Staff (1958) a summary log of the Oodnadatta bore (fig. 19a, p. 92) and an account of the recent stratigraphical observations (pp. 94-97, Rolling Downs Group) is given. Our *Aucellina* form series is from the "richly fossiliferous mudstone (Tambo Formation)" which comprises the top 425 ft. of the bore section. The individual members of the form series were found at the following levels:

Table 1.

Ranges of *Aucellina* Species in Bore near Oodnadatta.

Form F (youngest) was found on surface, probably in beds which are slightly younger than the beds of the top part of the bore section.
Form E, approximately from depth 100 ft. to 0 ft.
Form D, approximately from depth 235 ft. to 220 ft.
Form C, approximately from depth 300 ft. to 240 ft.
Form B, approximately from depth 345 ft. to 250 ft.
Form A, approximately from depth 375 ft. to 330 ft. (oldest).

All specimens described hereafter are deposited in the palaeontological reference collection of the consulting firm Geosurveys of Australia Ltd., Grenfell Street, Adelaide.

ON THE SYSTEMATIC POSITION OF *AUCELLINA* POMPECKJ.

The genus *Aucellina* was introduced by Pompeckj (1901) in order to accommodate a number of Middle Cretaceous (Aptian to Cenomanian) *Aucella*-like lamellibranchs which are known from various parts of the world. Of the two typical species named by Pompeckj *Aucellina gryphaeoides* (Sowerby) was subsequently designated as genotype by Marwick (1939).

The question of the systematic position of the genera *Aucella* Keyserling¹ and *Aucellina* has been the cause of much discussion among taxonomists. An exhaustive analysis is found in Pompeckj (1901). Although he did not really solve the problem his meticulous description and comparisons of the morphological features and those of related genera came to be the foundation of all later discussions. It seems the problem has recently been solved for good. Ichikawa (1958) demonstrates convincingly that *Aucella* and *Aucellina* belong to the family Aviculopectinidae (Etheridge jun., 1906) em. Newell, 1938, in which he has grouped them as subfamily *Aucellinae* (Fischer, 1887) em. Ichikawa, 1958, along with *Oxytominae* Ichikawa, 1958; *Aviculopectininae* Newell, 1938, and *Pseudomonotinae* Newell, 1938.

Whether *Aucellina* and *Aucella* should be regarded as members of the same subfamily may be of secondary importance, but nevertheless questionable. As Pompeckj (1901) has clearly shown, they are not as closely related as their superficial similarity in outline and other characters suggest. Their hinge features are evidently not the same. In *Aucella* there is a rather high degree of what may be called specialization when compared with the hinge features in the ancestral lineage which, as Ichikawa (1958) suggests—as did Pompeckj—includes *Pseudomonotis* Beyrich, 1862, and *Meleagrinella*, Whittle, 1902. *Aucellina*, on the other hand, has hinge characters which are in every respect closer to the ancestral *Meleagrinella* (= *Pseudomonotis* in Pompeckj, 1901) pattern than to that of *Aucella*. The latter is not likely to have been the forerunner of *Aucellina* except, of course, in the sense that the aucellid phenotype had evolved from meleagrinellid stock once before, i.e., in Upper Jurassic times. By the end of the Neocomian this specialized lineage had, however, died out, and *Aucellina* evolved during the Aptian independently, again showing clearly the ancestral hinge characters of *Meleagrinella*, i.e., characters which all later species of *Aucella* had largely lost. There is no evidence of intermediate forms which would link the specialized late forms of *Aucella* with the earliest representatives of *Aucellina*. Pompeckj (1901) has demonstrated this point, and since then nothing has been discovered that would contradict his findings. On the other hand, since the genus *Meleagrinella*—which has its earliest representatives in the Rhetian (Ichikawa 1958)—persists together with *Oxytoma* Meek, 1864, into the Upper Cretaceous, *Aucellina* could easily have been an offshoot in the Lower Cretaceous from that stock, as was *Aucella* at the beginning of the Upper Jurassic.

¹As regards the case *Aucella* versus *Buchia* Rouillier, 1845, see Jeletzky (1955).

The *Aucellina* lineage thus forms a phylogenetic group of equal rank as does the *Aucella* series or, for that matter, the predominantly Australian series of *Maccoyella* Etheridge jun., 1892, which stems also from aviculopectinid stock and arose at about the same time as did *Aucellina*. Phylogenetically this should be expressed by accommodating *Aucella* and *Aucellina* in separate subfamilies, i.e., *Aucellinae* (Fischer, 1887) em. Ichikawa 1958, and *Aucellininae nov.* of the Aviculopectinidae.

THE AUSTRALIAN REPRESENTATIVES OF AUCELLINA.

Species of *Aucellina* are among the commonest forms in eastern and northern Australian Albian formations. Because of the sessile and gregarious habits of the genus, one finds in places bands of real *Aucellina*-coquinites. The earliest Australian record is found in Etheridge sen. (1872) under the name *Avicula hughendenensis*. Etheridge jun. (1884) transferred this species to *Aucella*, and Pompeckj (1901) finally to *Aucellina*.

Pompeckj (1901) records, apart from *A. hughendenensis*, also *A. gryphaeoides* (Sowerby) from the Albian of Queensland. The species from the uppermost Albian near Darwin (Whitchouse, 1926b) received the name *A. incurva* by Etheridge jun. (1902). All three forms are similar morphologically, but they cannot be taken as variations of the one species, e.g., of *A. gryphaeoides*, as has been suggested to me verbally by colleagues. *A. incurva* is, on closer inspection, quite distinct from *A. gryphaeoides*. The latter's left valve has a far less prominent umbo, and its right valve shows not only a relatively larger anterior ear and a correspondingly narrower byssus slit, but also a fairly large posterior ear (or wing), a feature that is almost non-existent on *A. incurva*. Excellent figures of *A. gryphaeoides* are given in Woods (1905, pl. 10, figs 6-13).

Actually, the right valve of *A. incurva* is more like that of *A. aptiensis* (d'Orbigny), i.e., more or less obliquely circular (see Pompeckj, 1901, pl. 16, figs. 1-4). But these two species differ decidedly in the form of the left valve.

Closest to *A. gryphaeoides* is evidently Etheridge's *A. hughendenensis*. The only difference between these two lies in the latter's distinct radial riblets and striae on the left valve (in addition to the concentric ornament) and the typically more elongate, fan-like, obliquity of its right valve. On *A. gryphaeoides* radial ornamental elements are only rarely noticeable, and then on right valves and only very faintly. The ornament of *A. hughendenensis* recalls more that of *A. sancta-quirini* Pompeckj, but the latter's left valve has a slenderer and higher umbo and is in general outline more elongate oblique and slender, i.e., similar to *A. incurva*.

Consequently, it is better to keep the mentioned Australian species separate from each other and from overseas representatives of *Aucellina*, at least at the present stage of our knowledge of these forms. As will be seen presently, there is a fair measure of justification for such a cautious approach because the analysis of the *Aucellina* series from Oodnadatta suggests strongly that these and other forms are representing stages in a phylogenetic lineage. They are not geographical variations or subspecies, not "Standortsrassen" (local races of a species). These stages evolved through long times (several millions of years); when stage 3, for example, had been reached there were evidently no survivors left of stage 1. None of stage 2 were left when stages 4 or 5 were flourishing, and so on.

Wright (1958) has recently again emphasized the point of view of the palaeontologist as regards the concept of "species." The current definition of species as "a potentially interbreeding population" is rather wide open to criticism in its application to classification. It is a neontologist's concept which ignores the element of time. In the case of the *Aucellina* series, as in many other cases, we have no means of testing whether the early and late stages could interbreed. Placing all known Australian forms into one and the same species would, however, imply just that. This is surely a much too venturesome assumption. Consequently, as long as the evolutionary stages are in some or other way recognizable and separable morphologically they should be treated as distinct species. In the following demonstration of an *Aucellina* series this principle is adhered to, although—because of the still rather small number of specimens available—a *nomenclatura aperta* is applied.

THE AUCELLINA SERIES FROM OODNADATTA.

Six morphologically distinguishable types of right valves are now known from the Albian of northern South Australia. Left valves show, apart from size, scarcely any differences. If there are some, they have probably been obliterated by the effects of rock diagenesis. *Aucellina*, unlike many species of *Aucella*, is very thin-shelled and fragile. Left valves especially, being much more inflated than right valves, are always found crushed with their delicately twisted umbo flattened and the hinge characters distorted. The primarily flattish right valves, however, are commonly perfectly preserved and can be studied in every detail. They are shown in text fig. 1-6 along with the necessary descriptions.

AUCELLINA sp. nov. A. aff. *A. APIENSIS* (d'Orbigny).

Text fig. 1, (x 1½).



Aucellina sp. nov. A. aff. *A. aptiensis* (d'Orbigny).

Right valve, side and frontal aspects.

Description: A small species of the series. This right valve is moderately inflated, with rather distinct, slightly opisthocline (see Newell, 1938) umbo. Height and length are equal. Both anterior and ventral margins are evenly rounded. Posterior margin straight, forming an angle of between 90° and 100° with the cardinal margin, thereby enclosing an almost recto-triangular, clearly individualized, posterior ear (or area).

The anterior ear (or byssus ear) is long and slender. It is turned upward at an angle of 20-25° to the cardinal margin, as well as inward, i.e., against the left valve. The byssus slit between it and the prominently produced antero-cardinal wing (or ear) is wide and deep, reaching almost beneath the umbo.

The ornament consists of both radial and concentric striae and riblets. The radial ornament weakens towards the ventral and the posterior margins. Only concentric striae remain there. Fine concentric lamellae are discernible also on the byssus ear.

Comparisons: This right valve does not match any of the species described in the literature. None of these shows the up-and-inward twisted byssus ear and the subrectangular postero-cardinal margin. In its other features, especially the opisthoclinal to aclinial umbo, *sp. nov.* A. recalls to some extent *Aucellina aptiensis*. This is perhaps not surprising because the Australian form is, like d'Orbigny's species, apparently the oldest of a phylogenetic series. It certainly differs very much from *A. hughendenensis*.

The figured specimen comes from a depth of 370 ft. 8 in. in the bore. The vertical range of the species is given in Table 1.

AUCELLINA *sp. nov.* B. cf. *A. GRYPHAEOIDES* (Sowerby).

Text fig 2, (x 1½).



Aucellina *sp. nov.* B cf. *A. gryphaeoides* (Sowerby).

Right valve, side and frontal aspects.

Description: A small species of the series. This right valve is moderately inflated, with rather distinct, acline to slightly prosocline umbo. Height and length are equal. Anterior and ventral margins evenly rounded. Posterior margin straight, forming an angle of 115-125° with the cardinal margin, thereby enclosing a clearly individualized posterior ear. The anterior or byssus ear is fairly long, but not as slender as in the other forms. It is turned upward at an angle of 10-20° to the cardinal margin, as well as slightly inward towards the left valve. The byssus slit is wide and deep, reaching beneath the umbo. The antero-cardinal wing is produced with a sharply curved margin. The ornament consists of both radial and concentric striae and riblets. The radial elements weaken towards the ventral and the posterior margins, where only concentric striae and weak folds remain. The concentric (transverse) lamellae on the byssus ear are very weak.

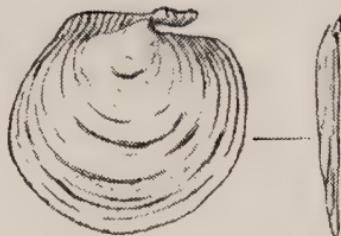
Comparisons: This form is very similar to *sp. nov.* A, but has a less up-and-inward twisted byssus ear, a greater postero-cardinal angle, a less dense radial ornament, and a nearly horizontally (instead of upward) opening byssus slit. Also, the antero-cardinal edge is less upward produced than in *sp. nov.* A. With its prosocline umbo and the consequent tendency to the typical aueellinid obliquity *sp. nov.* B begins to approach the phenotype of *Aucellina gryphaeoides* (see Woods, 1905, pl. 10, figs. 6c and 7b) although its postero-cardinal angle has not yet reached the obtusity of

the respective European species. In this it also differs from *A. hughendenensis*, whose elongate obliquity of the right valve is (as in *A. gryphaeoides*) much more pronounced.

The figured specimen comes from a depth of 298 ft. 6 in. in the bore. For the vertical range of the species see Table 1.

AUCELLINA sp. nov. C. cf. A. HUGHENDENENSIS (Etheridge sen.).

Text fig 3, (x 1½).



Aucellina sp. nov. C. cf. A. hughendenensis (Etheridge sen.).

Right valve, side and frontal aspects.

Description: A medium to fairly large sized species of the series. Right valve almost flat, with scarcely protruding acine to prosocline umbo. Length exceeding height by about 10%. Anterior and ventral margins evenly rounded. Posterior margin first continuing as evenly convex as the ventral margin but towards the cardinal margin developing a slightly concave re-entrant. The posterior ear is thereby well individualized. The postero-cardinal angle is typically well over 120°. In outline this species is therefore nearly circular with a long, straight, cardinal margin. The byssus ear is long and slender, forming a horizontal process that is *not* twisted against the left valve. The byssus slit is long and narrow, reaching to the small umbo. The antero-cardinal wing of the valve has a horizontal, straight, cardinal margin (almost as long and straight as the posterior cardinal margin), which curves gently into the anterior margin.

The ornament of concentric striae and weak folds is rather attenuated, and so are the fine lamellae on the byssus ear.

Comparisons: The flatness of the valve, the features of the cardinal margin, the slight concavity of the upper postero margin, and the increased average size as well as the height/length ratio of this *sp. nov. C* quite definitely foreshadow *Aucellina hughendenensis*. Yet it is equally obvious that *sp. nov. C* has not quite "arrived" there. Its only slightly prosocline umbo and consequently little oblique, almost circular, outline still recalls the forerunners A and B *sp. nov. C* is also individualized by the complete absence of radial elements in its ornament of the right valve. This characteristic feature may actually mean that *A. hughendenensis* proper, with its typical radial ornament, is an independent offshoot from A or B, i.e., that *sp. nov. C* is not in its ancestral stock.

The figured specimen comes from a depth of 296' 4" in the bore, and the vertical range of the form is shown in Table 1.

AUCELLINA HUGHENDENENSIS (Etheridge sen.)²

Text fig. 4 (x 1½).



Aucellina hughendenensis (Etheridge sen.)

Right valve, side and frontal aspects.

2 = Form D on Table 1.

Description: This well-known species belongs to the largest that have been evolved within the genus. The right valve is almost flat, with a very small umbo which is moderately to strongly prosocline. Length exceeding height by over 10%. Anterior and ventral margins broadly and evenly rounded. Posterior margin evenly convex in lower part but fairly strongly concave before reaching the cardinal margin, thereby delimiting a rather long, obtusely triangular posterior ear. Postero-cardinal angle 130-140° or even more. In outline this species is therefore fairly elongate oblique with a moderately long, straight, cardinal margin (about half the length of the valve). Except for being shorter in relation to the length of the valve, the features of the cardinal region are almost identical with those in *sp. nov. C*. Because of a slenderer byssus ear, however, the byssus slit appears somewhat wider.

The ornament consists of both radial and concentric elements. There are dense radial striae and fairly broad, but low, concentric folds. The concentric striae are of about equal density as the radials except on the posterior, marginal portion of the valve, where only concentric elements remain. Byssus ear finely lamellate.

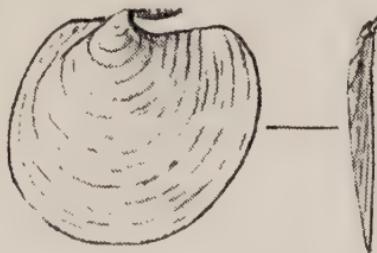
Comparisons: The affinities of *Aucellina hughendenensis* have been discussed in the introductory parts to this article. In our series it stands, morphologically speaking, between A/B on the one hand and C/E/F on the other, i.e., by uniting and carrying characteristic features of the two other groups it may be taken as "typifying" the whole series in its "temporal and geographical variation," and as far as Australia is concerned, in the sense of Wright (1958, p. 144, para. 2).

In itself, however, *A.hughendenensis* is probably a single offshoot from the main line (which was carried on through E and F to *A.incurva*, while *hughendenensis* died out before *incurva* appeared) that was very successful for a short time but left no descendants.

The typical *A.hughendenensis* as represented by text fig. 4 occupies only a small interval of Albian times. The figured specimen comes from a depth of 231' in the bore. The apparently very short range of the species is shown on Table 1.

AUCELLINA sp. nov. E. cf. *A. INCURVA* (Etheridge jun.).

Text fig. 5, (x 1½).



Aucellina sp. nov. E. cf. *A. incurva* (Etheridge jun.).

Right valve, side an' frontal aspects.

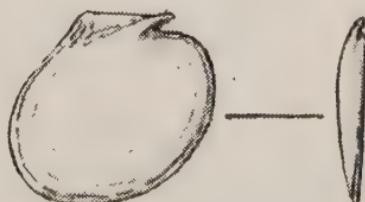
Description: This species is of moderate to large size. The right valve is only very slightly inflated. The only moderately prosocline umbo is small but well defined, sharply pointed, and protruding a little above the cardinal margin. Height of valve only slightly less than length. Posterior, ventral, and anterior margins evenly rounded. Antero-cardinal edge sharply rounded, almost angular. Posterior wing small and rounded, forming only a narrow, elongate area behind the umbo. Byssus ear slender, fairly long, horizontal. Byssal slit deep and narrow, reaching beneath the umbo. Anterior cardinal margin long, a little concave, about twice as long as the byssus ear. Anterior wing of valve prominently extended, relatively much larger than in any of the other forms. In outline this form is thus subcircular, but conspicuously inequilateral with the umbo set backward. The cardinal margin as a whole is long (about $\frac{2}{3}$ the length) and slightly concave, without the typical en-échelon step-down under the umbo (in side view) of the other species. Byssus ear parallel to cardinal margin, not twisted towards left valve. Ornament of extremely fine concentric striae or none at all. Very fine lamellae on byssus ear.

Comparisons: This species clearly approaches *Aucellina incurva* especially in its enlarged anterior wing and the loss of the angularity of the postero-cardinal edge. However, because of its well-defined umbo and its subcircular rather than obliquely elongate outline it remains distinct from *A. incurva* (Etheridge jun., 1902, pl. 7, figs. 22, 24, 27).

The figured specimen comes from a depth of 73' 5" in the bore. The range of the species is shown on Table 1.

AUCELLINA, sp. nov. F aff. *A. INCURVA* (Etheridge jun.).

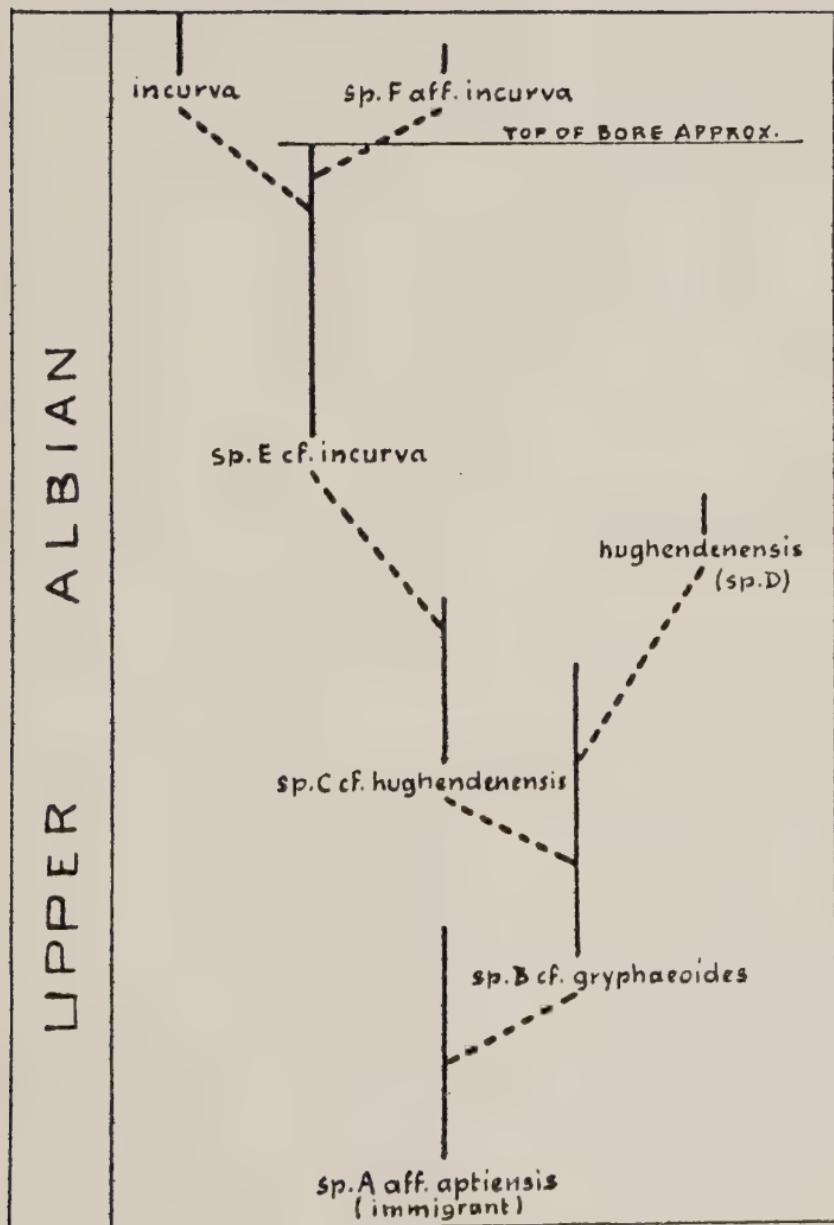
Text fig. 6, (x 2).



Aucellina sp. nov. F. aff. *A. incurva* (Etheridge jun.).

Right valve, side view.

Description: This is a small species of the series. The right valve is flat or only slightly inflated. The poorly defined umbo is strongly



Text fig. 7.

PHYLOGENY OF AUSTRALIAN AUCELLININAE.

Note: Branching to the right means tendency towards phenotype of *Aucellina hughendenensis*.

Branching to the left means tendency towards phenotype of *Aucellina incurva*.

prosocline. Height of valve only slightly less than length. Anterior and ventral margin broadly and evenly rounded, posterior margin straight or faintly concave towards cardinal margin, forming an obtuse angle (over 130°) with the latter and thereby enclosing an elongate, narrow, triangular posterior ear similar to that in *sp. nov. C.* Byssus ear short, more like a simple, sharp fold than a spoon-shaped process. Byssal slit rather short and narrow. Anterior wing of valve rather small with evenly, broadly rounded antero-cardinal end. Posterior portion of shell conspicuously larger than anterior, umbo set forward. In outline this form is therefore moderately elongate oblique. No ornament noticeable.

Comparisons: Since this form was found on the surface in a quite different state of preservation (limonite replacement) from those in the bore comparison is not easy. In general outline it resembles *Aucellina hughendenensis*, but the short and simple byssus ear and the absence of any ornament may indicate closer relationships to the species E and C, i.e. to the lineage which seems to end in *A. incurva*. The exact stratigraphical position of this form F is unfortunately not known, but it is certain that it is younger than species E not only because F was not encountered in the bore, but also because field evidence suggests that the gypsiferous beds which contain F are probably younger than the youngest beds in the bore. These circumstances prompt me to leave *sp. nov. F.* in the *incurva* group.

The figured specimen comes from the gypsiferous shales just north of the Arkaroola Road about fifteen miles south-west of Oodnadatta.

SUMMARY AND CONCLUSIONS.

The afore described six species of *Aucellina*, in this case all characterised by the features of their right valves under *nomenclatura aperta*, show that variations in shape and size with time are very considerable in this genus even within a comparatively short geological time interval such as the upper Albian. It is understood, of course, that additional drilling in the Artesian Basin may not only bring about some corrections to the range in time of the individual members of this *Aucellina* series, but may also produce a number of intermediate forms which may appear to close some of the as yet quite astounding "gaps" between our six species. Yet this cannot alter the fact that rapid phenotypic changes take place on what I consider to be the specific level. The discovery of some more *Aucellina* forms could possibly make the taxonomic classification of the members of this series more difficult because transitional forms might have to be accommodated. Yet this may not prove to be problematical.

It all depends at what time such "transitional forms" make their first appearance. A form which appears morphologically intermediate between e.g. our species A and B will spell taxonomic trouble for A and B only if its first appearance is before or, at the latest, at the same time as that of B, i.e., if the new form is transitional also in the temporal sense. If it appears after B, however, or even after C or D, it must be classified as a separate species. It is most likely a homocomorph, a throw-back, further along the lineage, which means that it had no chance of interbreeding with the phenotypically similar ancestors—the latter were already extinct. The "transitional form" must stand on its own in such cases.

This is also, I presume, what Wright (1958) means by "phylogenetical thinking," and I cannot but agree with him. One understands why he repeatedly criticised neontologists for some of their classification efforts which did not allow for the element of time.

To conclude this paper on the Australian *Aucellina* series, the results are presented in text fig. 7 in the form, still tentative, of course, of a phylogenetic interpretation.

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THE ANIMAL OF *AUSTROGINELLA JOHNSTONI* (Petterd).

By FLORENCE V. MURRAY, M.Sc.*

(Text fig. 1-2.)

Marginella johnstoni (Petterd), 1884, *J. Conch.*, 4, p. 143.

Adult shell: 7 mm. to 10 mm. in length.

Living specimens of this species were located by Mr. C. E. Collinson near McCrae, Port Phillip Bay, Victoria, during a field day organized by the Malacological Society of Australia on 29/3/1959. Just beyond low water, they were inhabiting an area which extended east-west for at least a mile, and were thickly populated in some places but sparse in others. Some were on the surface, but mostly they could be found by feeling for them at the end of their six-to-eight-inch long tracks, or by screening the sand with a small handsieve. They were extremely lively, quickly climbing out of the collection jars; some kept for observations lived for six weeks in a small petri dish of sea-water and sand changed only several times.

The animal is pale cream in colour when contracted, but translucent in extension, with dark brown, orange, yellow and white pigmentation.

The foot, when fully expanded, measures 17 mm. x 12 mm. (shell 10 mm. x 6 mm.), and generally resembles a lace mat (text fig. 1). It is furrowed anteriorly, semi-transparent, and dappled with large groups of white spots interspersed with smaller groups of orange or yellow spots.

The mantle is thin, transparent, smooth, and splashed with dark brown, orange and white, the latter predominating. It completely envelopes the shell, encroaching in three distinct lobes as indicated in text fig. 1. The left and largest lobe passes over the top of the body whorl and meets the smaller anterior right lobe well over on the right side; the posterior right lobe wraps round the apex, covers the spire and extends up and over the back of the body whorl to meet the other two lobes, the margins of the three lobes always meeting in the same positions.

The siphon is held erect, and when fully outstretched reaches 5 mm. in length. Tubular in shape, it gapes widely down the ventral line; it is bright orange or yellow at the anterior end, otherwise mainly white speckled with dark brown.

The head and tentacles are transparent, the latter having a central core harbouring pigment specks. Conspicuous black eyes are situated in swellings at the outer bases of the tentacles.

A retractile, tubular proboscis (text fig. 2) emerges from the under part of the head, just above the sole of the foot, and swings round to protrude from behind the right tentacle. It gropes about, changes shape, and is capable of extending nearly half-way down the body. On the slightest disturbance it quickly contracts back into the mouth opening.

Male animals have a large penis (text fig. 2) coming from the right side of the head.

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Austroginella johnstoni (Petterd).



Text fig. 1.

Dorsal view of living animal with foot expanded, mantle encroaching over the shell, and proboscis protruding. Actual size of shell: 10 mm.
x 6 mm.



Text fig. 2.

Side view of part of the body of male animal (removed from shell) with mantle (m) folded back to expose penis (p), siphon (s), proboscis (pr).

NOTES ON LITTORINID NOMENCLATURE

By DONALD F. McMICHAEL, Ph.D.*

A revision of the nomenclature of the Australian littorinid molluses is necessitated by Guiler's recent paper (1958) on the Tasmanian species of *Melarhaphe*. As the littorinids are key members of the littoral fauna used as marker species in studies of littoral zonation, it is important that their nomenclature should be stabilized. Guiler claimed to show that *Melarhaphe* was not an acceptable genus for the two Tasmanian species, usually listed as *Melarhaphe unifasciata* (Gray) and *M. praetermissa* (May). He considered that these species were not generically separable from *Littorina* s.s. It was considered necessary to check the data presented by Guiler and to reach some definite conclusion regarding the validity of the genus. In conjunction with this study, recent work by Abbott (1954) necessitates a revision of the nomenclature of the common *Nodilittorina*.

Guiler's paper contains a number of statements which are incorrect, so the essential facts are given here. The genus *Littorina* Ferussac 1822 was introduced on p. xxxiv of the *Tabl. Syst. des Moll.*, without included species. Iredale (1912) and other workers had assumed that Rang was the first to designate a genotype for *Littorina*, (1829, *Man. Mollusques*, p. 185), the species selected being *Nerita littoralis* L., (= *Turbo obtusatus* L.). However, Winkworth (1922) and Bequaert (1943) have shown that there is an earlier type selection for *Littorina*, by Blainville (1828), who was the first to refer definite species to *Littorina*, and selected *Turbo littoreus* Linne as type species. This, of course, must be accepted, and alters the concept of *Littorina*, because *obtusata* L. is a rather aberrant

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pecies. The latter species was made the type of the genus *Neritrema* *cecluz* by subsequent designation (Dall, 1909), so that generic name will be available for the *obtusata* series.

Iredale first introduced the name *Melarhaphe* into Australian molluscan nomenclature in 1912, and it has been generally adopted since then. Elsewhere it has been used either generically or subgenerically under *Littorina*, but, surprisingly, reinvestigation of the name reveals that it was never validly introduced and is hence unavailable. Iredale (1912) cited the original introduction of *Melarhaphe* as follows: "Commonly quoted as of Muhfeldt, this name was introduced into literature by Menke (*Synops. eth. Moll.*, 1828, p. 23), thus: *Paludina glabrata* Zgl. (*Turbo coerulescens*, Lin., *T. rupestris* Chabr., *Melarhaphe glabrata*, Mhlfld.)." Iredale and his workers, including Dall (1909), Winkworth (1922) and Bequaert (1943) have accepted this to be a valid introduction of the genus with the type species by monotypy *Paludina glabrata* Pfeiffer = *L. neritoides* (L.).

However, at the Paris Meetings of the International Congress of Zoology, 1948, it was decided that the publication of a generic name merely as the generic component of a binomen cited in the synonymy of nominal species, did not constitute sufficient indication to make the generic name available. This decision has now been incorporated into the new rules, and therefore the introduction of *Melarhaphe* (which exactly falls within the meaning of the above decision) was invalid, and the name is not available. It is therefore necessary to find the first valid name for the taxon which has been known as *Melarhaphe*, that is, the group of species allied to *Littorina neritoides* Linne. This could be either another name with a species of "Melarhaphe" as type species, or the first valid introduction of *Melarhaphe* which would fulfil the conditions of availability.

A number of alternative introductions of *Melarhaphe* or slight modifications of this name are listed in the various "Nomenclators" such as Herrmannsen, Sherborn and Neave. It has not been possible to check all of these because of the unavailability of literature, but it appears that the generic name to be adopted will be *Melarapha* Cristifori and Jan, 1832. I am indebted to Dr. Joseph Bequaert for the information that this generic name was validly introduced as a division of *Paludina*, without characters, but monotypic for "*Paludina glabrata* Meg. (= Muhfeldt)" which correctly is *Paludina glabrata* Pfeiffer = *Littorina neritoides* (L.). Until it can be shown otherwise, *Melarapha* Cristifori and Jan will serve as an acceptable substitute for *Melarhaphe* Menke, as it differs only slightly in spelling and pronunciation so that its use will cause little confusion."

We then have to consider two generic names, *Littorina* Ferussac, with *littoreus* Linne as type, and *Melarapha* Cristifori and Jan, with *neritoides* Linne as type. Guiler states that *Melarhaphe* was never followed in Europe, and then proceeds to quote Quoy and Gaimard (1833), who used *Littorina* for *diemenensis*. This is hardly surprising, for in 1833 restricted genera like *Melarhaphe* were seldom used. Guiler also cites the Conchological Society's list of British Mollusca, in which *Littorina* is used for *obtusata* L. This again is not surprising, for at that time *obtusata* was thought to be the type species of *Littorina* and could not have been cited otherwise. In any case, *Melarhaphe* was never applicable to the *obtusata* series. Finally, Guiler cites Moore's (1937) usage of *Littorina* or *littorea* L., and Thiele's omission of *Melarhaphe* in Kukenthal's

Handbuch der Zoologie. In both cases his argument is incorrect, for *littorza* L. now known to be the type of *Littorina*, has never been considered to belong with *Melarhaphe*, and Thiele (1929) did use the name as a subgenus of *Littorina* in his *Handbuch der Systematischen Weichtierkunde*, if not in Kukenthal's *Handbuch*!

Guiler omitted to mention that Winkworth (1922) had adopted *Melarhaphe* as a full genus for the British *neritoides*, and that more recently Bequaert (1943) had allowed the name subgeneric status for western Atlantic species. Abbott (1954) has presented some data on the *Melarhaphe* subgenus of *Littorina*, which indicates that it might well be considered as a full genus. (Obviously, since *Melarhaphe* is to be replaced by *Melarapha*, which has the same type species, argument about the taxonomic status of *Melarhaphe* applies equally to *Melarapha*.)

What then is to be the fate of the Australian species commonly referred to *Melarhaphe*? Are we to adopt *Littorina*, using *Melarapha* subgenerically or are we to adopt *Melarapha* generically? This is essentially a matter of opinion, depending on the value placed on the characters separating the two groups. In my opinion, *Melarapha* is a well characterised group within the *Littorinidae*, distinguished by its peculiarly straight and flattened columellar, and apparently also by its egg capsule and penis structure. I therefore propose to retain *Melarapha* for such species as *unifasciatus* Gray and *praetermissa* May.

In reading Abbott's (1954) paper on Atlantic periwinkles, I noted again that the name *tuberculatus* was in use for the western Atlantic *Nodilittorina* as well as the Australian species. I had previously noticed this double usage, but at the time set it aside for further study. Abbott's paper reveals that the Atlantic usage is based on an introduction of *Littorina tuberculatus* by Menke in the *Synopsis Methodicum Molluscorum*, 1st Edition, 1828, p. 25, where reference to Gmelin's *Trochus nodulosus* var *minor* is made. The latter is an invalid name for the West Indian *Nodilittorina*, which differs in size and other characters from the Australian species. Australian workers first adopted *tuberculatus* Menke after Iredale 1924 had shown that Menke in *Verz. Conch. Samml. Malsburg*, p. 10 had used *tuberculatus* for *Trochus nodulosus* Gmelin s.s., that is, the Pacific form. Since the date of the latter paper is 1829, it is anticipated by Menke's 1828 usage, and hence the name *tuberculatus* will have to be left with the West Indian species.

This being the case, we must choose the next earliest name, which appears to be *Littorina pyramidalis* Quoy and Gaimard 1833, which Hedley (1913) used in his Check List, and so the species will return to *Nodilittorina pyramidalis* (Quoy and Gaimard). Abbott (1954) gives a synonymy for the species, which however requires further investigation. A revision of the eastern Australian *Littorinidae* is anticipated, and the various species will be discussed more fully there.

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COMMENTS ON THE AUSTRALIAN UMBRACULACEAN MOLLUSCA

By ROBERT BURN*

(One text figure.)

For many years two Australian species of molluscs have been referred to the genus *Umbraculum* Schumacher 1817: the reasons given hereunder show why this is incorrect, and a solution to the problem is offered. The present writer, while engaged on an anatomical study of the family Umbraculidae, found that he could not obtain preserved material of the smaller Australian species, *U. corticalis* (Tate) 1889. Thus the observations made here are based purely upon shell characters, the foremost being the muscle scar inside the shell.

From the careful examination of a large series of *Umbraculum* shells, it was observed that the internal scar of the columellar muscle was complete in every case with the exception of the species, *U. corticalis* (Tate). Here the columellar muscle was open on the right side of the shell, and another smaller muscle, the intermediate suspensor muscle, nearly filled the gap between the ends of the columellar muscle. Research through literature showed that this gap in the columellar muscle and the presence of an intermediate suspensor muscle was characteristic of the genus *Tylodina* Rafinesque 1819 from the north Atlantic and north Pacific Oceans. Together with the genus *Tylodinella* Mazzarelli 1897, *Tylodina* comprises the family Tylodinidae, both genera differing from *Umbraculum* in that the columellar muscle is incomplete. A key to the families and genera

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of the suborder UMBRACULACEA is appended here in order to set out the various characteristics stated above.

A. Columellar muscle complete.

Family Umbraculidae.

Body grossly tuberculate. Shell smaller than animal.

Umbraculum Schumacher 1817.

B. Columellar muscle incomplete, open on the right side.

Family Tylodinidae.

i. Intermediate suspensor muscle present. Shell generally smaller than animal. Radula with rhachidian.

Tylodina Rafinesque 1819.

ii. Intermediate suspensor muscle absent. Shell larger than animal. Radula without rhachidian.

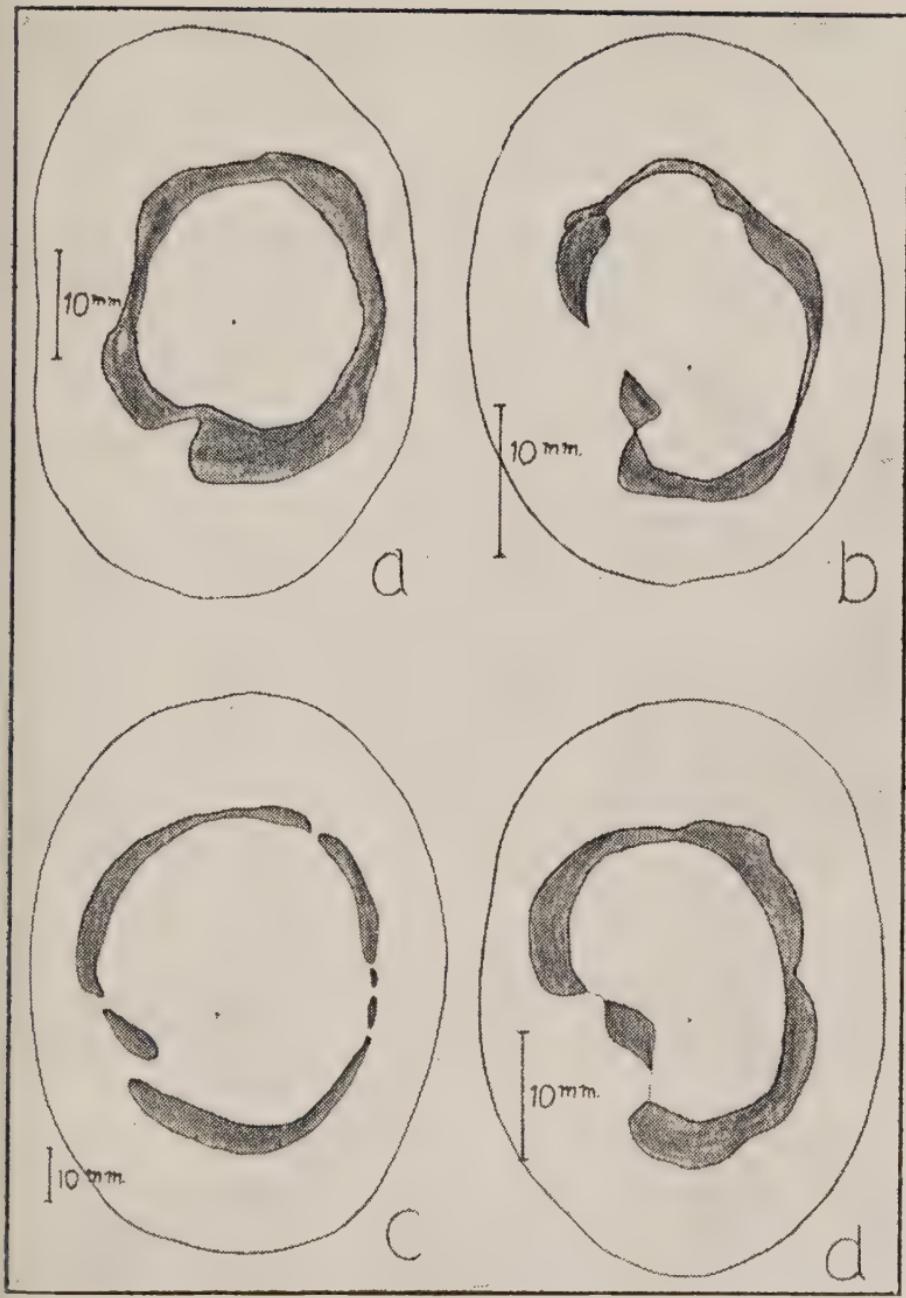
Tylodinella Mazzarelli 1897

Through the kindness of Dr. Bengt Hubendick of the Riksmuseum, Sweden, the author was able to obtain sketches of the columellar muscle formations of two differing species of *Tylodina*. These are reproduced as figures *b* and *c* on the accompanying text figure. They are respectively *b* — *T. citrina* Joannis 1834 from Puerto de Orotova, Canary Islands and *c* — *T. fungina* Gabb 1865 from Laguna Beach, California. Figure *a* represents the type species of the genus *Umbraculum*, *U. sinicum* Gmelin from Mauritius and shows the complete columellar muscle scar on the underside of the shell. *U. corticalis* (Tate) is represented by figure *d* and its close similarity to figures *b* and *c* can easily be seen.

Thus here *U. corticalis* (Tate) is removed from *Umbraculum* and transferred to *Tylodina*, becoming *Tylodina corticalis* (Tate). This species is by far the largest of the Tylodinids, attaining a length of 45 mm. in the largest shell yet examined by the author.

It is also worthy of note that the species *Umbraculum botanicum* Hedley 1923 from New South Wales should be reduced to a synonym of the type species, *U. sinicum* Gmelin. Likewise the author feels that all other species of *Umbraculum* should be reduced to the synonymy of *U. sinicum*, and the genus made monotypical with one circumtropical species, the type. There appear to be no differences, either conchologically or anatomically, in any of the many species attributed to the genus and as such each reverts to the synonymy of the type. The many species have arisen through various authors not having the actual animals to study and creating specific differences on colour and shell shape when both these are extremely variable, the extremes can often be found side by side in the one locality. The study of the animals is the only solution to this problem. Results of the anatomical studies of *U. sinicum* will be presented at a later date.

The author wishes to thank Dr. Bengt Hubendick of the Riksmuseum, Sweden, for sketches and information on species of *Tylodina* not available for study in Australia; the National Museum of Victoria for making available its entire collection of UMBRACULACEA; the South Australian Museum for forwarding a complete series of *Tylodina corticalis* (Tate). To Mrs. D. I. Hartley, Mr. C. Gabriel and Mr. C. Collinson, all of Melbourne, go the author's thanks for making their personal collections of UMBRACULACEA available to him.



Explanation of Text Figure.

a—*Umbraculum sinicum* Gmelin from Kurnell, N.S.W.

b—*Tylodina citrina* Joannis from Puerto de Orotova, Canary Islands.

c—*Tylodina fungina* Gabb from Laguna Beach, California.

d—*Tylodina corticalis* (Tate) from South Australia (precise locality not stated).

In each figure the underside of the shell is depicted and the muscle scars shaded.

A NEW GENUS AND SPECIES OF LAND SNAIL FROM NORTH QUEENSLAND

By DONALD F. McMICHAEL, Ph.D.,*

(One text figure.)

While the marine mollusca of eastern Australia are studied by many malacologists, both amateur and professional, only a few collectors take an interest in the terrestrial mollusca. However, collecting land snails can be very rewarding from a scientific point of view, for the terrestrial mollusca are still not well known, and many species remain to be described, while the study of distribution has hardly begun. The present paper deals with one new species which appears to be quite distinct from any known Australian group.

This interesting discovery was made by a New Zealand collector, Mr. L. Price, of Kaitaia, who visited Australia between 1956 and 1959, collecting mainly in Queensland. He obtained a large number of species from many localities, and a report on some of these is in preparation. The present species immediately stood out because of its flattened, multi-coiled shell, and at first sight recalled a miniature *Trochomorpha*. However, that genus does not occur in Australia, and the new species differed in a number of important ways. The glassy texture of fresh shells and the absence of well-developed sculpture marked the shell as zonitid in the broad sense. The only Australian species at all comparable in size and shape are the two Queensland species of the genus *Theskelomensor* Iredale, (*T. lizardensis* (Pfeiffer) and *T. creon* Solem.). These are of doubtful affinity, but in any case comparison shows that this genus and the new species are quite different. The latter is not so sharply keeled, and lacks the peripheral threads and ribbed sculpture of *Theskelomensor*.

A number of dead shells were collected, but living animals could not be found. Eventually the true family position of this species may be revealed by anatomical and radula study. Temporarily it may be assigned to the family *Helicarionidae*, following Baker's scheme for Pacific Islands zonitids, in which he includes Iredale's family *Microcystidae*. The latter includes a number of Queensland shells which are nearest to the present species.

CRATERODISCUS PRICEI gen. et. sp. nov.

Description: Shell small, the largest specimen 5.3 mm. major diameter, 4.9 mm. minor diameter, discoidal, the maximum height 2.4 mm.; texture smooth, glossy zonitid facies, deeply and broadly umbilicate; whorls six, tightly coiled, sutures impressed; shell almost planate above, whorls shouldered, the sides flattened, whorls rounded beneath; shoulder bluntly keeled, the maximum diameter of the body whorl at the shoulder, the sides of the whorls receding ventrally; apical whorls smooth, adult whorls obscurely sculptured with fine lines of growth which are sometimes a little coarse and regularly spaced, more often irregular and obsolete; aperture semi-lunar, lip simple, sharp; colour translucent yellowish-white. Animal and radula unknown.

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Dimensions:

	Major Diameter	Minor Diameter	Height
Holotype	4.7 mm.	4.4 mm.	1.9 mm.
Paratype	4.5	4.1	1.7

Type Locality: Hypipamee Crater, Atherton Tableland, North Queensland. In leaf mould, common, October 1958.

Types: The holotype and five paratypes are in the Australian Museum, Register Numbers C. 62650 and 62651 respectively. Eight additional paratypes are in Mr. Price's collection.

Remarks: *Craterodiscus pricei* is the type of the genus *Craterodiscus* by monotypy. The genus differs from other genera of Helicarionidae in its discoidal form, shouldered whorls, combined with the broadly open umbilicus and lack of notable sculpture.

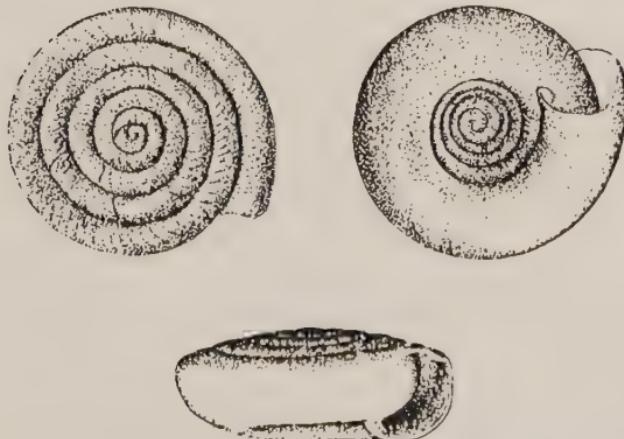
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Craterodiscus pricei McMichael. Holotype: Dorsal, Ventral and Apertural Views. B.P. Bertram del. Magnification X 6.

THEY ALL BEGAN WITH A SHELL

By A. W. B. POWELL, Ph.D.*

Money, purple dye, oil lamps, window panes, a marriage custom, certain religions and even a security pact—a curious assortment of ideas, yet all had their origin in some kind of shellfish.

When the human race was young shellfish played a much more important part in man's affairs than now, for without exercising either strength or skill coast-dwelling primitive man had a readily available supply of wholesome food in mussels, clams, oysters and whelks. The discarded shells which soon littered the camp sites of early man provided a durable material for the fashioning of rough scrapers, knives and fishhooks.

From these simple utilitarian beginnings emerged certain arts, beliefs and customs, some of which I shall now describe. Actually our monetary system and the marriage custom of throwing rice, or its modern equivalent, confetti, had a common origin in the tropical cowry shells. These shells were cherished by the ancients as symbols of good omen and in particular as fertility and regeneration charms. Collection of numbers of these shells became a necessary part of a bridal dowry, in ancient times, a custom that still prevails in the alternative fertility charm symbolised by the grain of rice. A parallel development was the employment of cowry shells as exchange for goods, an improvement on direct bartering methods.

Down the centuries cowry shell currency became standardized in the Orient, particularly in India and later in Africa. One species (*Cypraea moneta*), the money cowry, was used, and its value ranked in India during most of the nineteenth century at 3800 shells to the rupee, then equivalent to 2/- sterling.

There is a story of an Englishman resident in Bengal about 1820 who paid for the erection of his bungalow entirely in cowry shells. The sum involved was 4000 rupees, and the number of shells necessary for the transaction was sixteen million.

It requires no great stretch of the imagination to realize the significance of our slang term "shelling out," just as the term salary dates back to the early Eastern practice of payments in salt.

Many other kinds of shell money are known, but all differed in that they were manufactured, the labour and finish bestowed upon the product contributing largely to its worth.

The North American Indians had two forms of shell money, wampum of the eastern tribes, and alheochick of the Californian Indians. Wampum featured in the early days of the Hudson Bay fur trade until the company changed to a bartering method, using blankets. This form of money consisted of cylindrical beads ground from clam shells, and its value was 9d. to 1/6 per yard. The currency was declared illegal in 1862 owing to depreciation caused by unscrupulous early settlers who devised mechanical means of mass producing wampum.

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It seems that an ancient Scot first devised a receipt from shells, for an ancient legend discloses that an ordinary cockle was used for the purpose, the parties to a transaction each retaining one half of the shell. If you try to match odd valves of ordinary cockles, you will soon find that it is next to impossible to fit two disassociated halves that did not grow together.

Next we come to Tyrian Purple, a celebrated dye with the ancient Mediterranean peoples, which was manufactured from the crushed bodies of a sea shell (*Murex brandaris*), probably the first dye to be permanently fixed to wool and linen.

The art of purple dyeing probably originated in Babylon, but it was the Phoenicians who exploited the process, and their trade supremacy of the times was built up to a considerable extent by the distribution of this costly commodity.

It took thousands of shellfish to make an ounce or so of dye, and this, coupled with a long and intricate process, made the product so expensive that only the very wealthy could afford the coveted purple robes. In time the wearing of purple became the restricted privilege of kings and priests, and so to-day we have the survival of the idea in royal purple and the Cardinal's robes.

Another article that had a primitive beginning based upon the use of a shell is the ordinary oil or kerosene lamp. It was simply a spiral shape of shell suspended horizontally with strings. The cavity contained oil, obtained by rendering down sea birds and whale blubber, and in it was immersed a wick that protruded over the edge of the shell. This kind of lamp persisted in all its simplicity until a few decades ago at the Shetland Islands. I was much interested to note one of these lamps in one of the interior shots in the film "Man of Arran" which was shown in Auckland about twenty years ago.

Long before Western civilization became acquainted with the use of glass windows, the people of southern China and Malaya used the thin, semi-transparent *Placuna* shell as window panes.

Such windows persist in the Philippines, where almost every house, and even the modern multi-storied Manila hotels have their shell windows. The flat *Placuna* shells are trimmed to three-inch squares and set in latticed cedar frames. They are only semi-transparent, but admit an abundance of mellow light without heat.

Prior to the accidentally devised blotting paper, handwriting was tried by means of "pounce," a dusting powder ground from the internal shell of the cuttle-fish, a near relative of the octopus. The same creature has the ability of clouding the water with a brownish substance to facilitate escape from their enemies. This substance provided the pigment for the manufacture of the artists' colour, sepia.

A child of to-day places a sea shell to the ear and is momentarily fascinated by the illusion of sounds of sea and surf that issue from the shell. The child of to-day, however, knows that there is bound to be a simple explanation for this minor miracle, and either dismisses the problem or with a flash of intuition associates it with the amplifying apparatus of the familiar radio. To the child-mind of ancient man these sounds of the sea associated with the shell had a much deeper significance. To

him this was the voice of the god of the sea—and thus the shell trumpet became the logical instrument for invoking any deity associated with the sea.

Actually the phenomenon is capable of simple explanation, for the shell does act as an amplifier of those sounds that are too weak to be picked up by our unaided ears. Similar but less perfect reception of these sounds may be gained by simply arching the palm of the hand over an ear.

The use of shells as trumpets is very ancient, and has become almost world-wide. They were used by primitive man away back in Neolithic times, and they are still in use by the natives of Melanesia and Polynesia.

The Maoris fashioned trumpets by cutting off the end of the spire of a shell and adding an elaborately carved wooden mouthpiece, but the Melanesians simply bored a round hole in the side of the shell at a short distance from the tip of the spire. Of the two methods, the latter seemed to produce the more resonant, deeper and better carrying note.

“To blow one’s own trumpet” undoubtedly originated in the early days of the shell-trumpet. Even in Japan, where shell trumpets were used in civil affairs for issuing warnings of fires, riots and robberies, there is the current expression, “Ano hito wa hora wo-fuku,” which means—he blows the triton horn, or more concisely, he is bragging.

In India a different kind of shell, the “chank,” is widely used as a trumpet with special religious significance. The Brahmins recite a prayer to their god, Vishnu, who is usually depicted with a “chank” shell in his hand. All devout Brahmins possess one of these shells, which is held in the hand as the prayer to Vishnu is recited. So great is the demand for these shells in India than an important fishing industry operates for this purpose alone. Bangles and feeding spouts for babies are fashioned from the shells also, still with the same devout purpose in view.

Postage stamp collectors will find a conventionalized representation of the “chank” as the central motif in the design of the stamps of the Indian Native State of Travancore.

We must now consider the higher significance of shells with certain people. For instance, the late Dr. Malinowski, who studied the culture of the natives of the D’Entrecasteaux archipelago off the eastern end of New Guinea, records an extremely interesting social system which he termed the “Kula Ring.”

This is based primarily upon the circulation of two articles of high value but of no real use; they are arm-shells made from a large *Conus* shell and necklets of red shell-discs.

The necklets, Soulava, always travel clockwise, and the arm-shells, Mwali, in the opposite direction. The exchange of these articles occasions much ceremony, and the real business of the exchange of useful commodities is transacted later between the people that have entered into partnership through the Kula exchange. Each partnership becomes a firmly established life-long affair. An old chief may in the course of his life establish relationship with a hundred or more partners in neighbouring islands, and the value of this can be readily understood when it is explained that all partners in the Kula are under mutual

obligations to trade with each other, as well as to offer protection, hospitality and assistance whenever needed.

An example of a kula expedition is as follows: A fleet sets sail from Sinaketa bound for the island of Dobu, to the south. An intermediate stay is made at the Amphlett Group, but the fleet soon sails again for Dobu, where the real ceremony of the kula takes place. Here the Dobuans present their visitors with Soulava necklaces made of *Spondylus* shells, and later much trading takes place.

All the transactions in Dobu concluded, the party receive their parting gifts, sail back, and in due time, after a year or so, the Dobuans will make their return expedition to Sinaketa, with exactly the same ceremonials and magic. On this expedition, they will receive some *Conus* armshells in exchange for the necklets previously given, and others, as advance gifts towards the next Kula transaction.

Every really good Kula article has its individual name; round each there is a sort of history and romance in the traditions of the natives.

That the kula articles are seldom worn even as ornaments and are not of any real use may make us wonder why these natives place such store upon such articles. However, Dr. Malinowski, who has written at great length upon the kula system, points out an interesting analogy that will help us to understand the natives' point of view.

He described a visit he made to Edinburgh Castle, where he was shown the Crown jewels, too ostentatious, ungainly and valuable to be worn, yet they are greatly prized for the sheer sake of possession.

Until recent years the Melanesians relied greatly upon shell as a material to fashion a variety of everyday articles. One shell, the baler or melon shell (*Melo*) served as a pot to cook the enclosed animal, by placing it in hot embers; the same shell, as the first name implies, made an excellent canoe baler. The prized item, however, was the giant clam (*Tridacna*) of the coral reefs, which sometimes attains a weight of 500 pounds and a length of over three feet. This shell, by its strength and toughness, provided the raw material for the manufacture of adzes at the Gilbert Islands, which, being of coral formation, furnished neither rock nor durable materials other than shell from which tools and weapons could be fashioned. Thus they had adzes, gouges, scrapers, drills and utensils all fashioned from shell.

With the Maori people a great variety of shellfish were used as food, but only the shell of the paua and one or two others were used. The use of paua was largely decorative for forming the flashing baleful eyes of carvings, but it served a very useful purpose also in the making of fishhooks, particularly trolling spinners for the capture of kahawai and kingfish.

In our modern civilization not many shellfish serve purposes other than for food. Most of the early usages have been supplanted by more efficient and cheaper synthetics. It probably cost the equivalent of hundreds of pounds to make an ounce of purple dye in Phoenician times—to-day the same amount of dye can be produced by chemical means for a fraction of a penny.

One shell art still survives in the carving of cameos. Originally cameos were carved from banded onyx, a form of agate, but now a West

Indian shell (*Strombus gigas*) is used, and most of the carving is done in Italy.

A use of shellfish that will probably never die in spite of synthetic substitutes is the fashioning of pearls into articles of personal adornment.

A clever Japanese, Dr. Mikimoto, originated the now thriving Japanese pearl culture industry, the basis of which is the introduction of a small foreign body into the living oyster, which year by year coats this cause of irritation with successive layers of pearl until a fine gem results. A pearl, however, can be of no better quality than the mother-of-pearl of the oyster that forms it, and unfortunately for the Japanese the quality of the mother-of-pearl in their oyster is inferior to that of the Australian, Ceylon and Pacific Island oysters.

Certain fresh-water shells produce pearls also, and for many centuries a Scottish pearl industry was carried on. This industry is quite ancient—in fact, stories of fabulous pearls from Britain was one of the minor inducements behind Caesar's invasion of Britain.

RADULAE OF FOUR GASTEROPODS FROM SOUTH AUSTRALIA AND NEW ZEALAND

(Text figs. 1-4.)

By TADASHIGE HABE, Ph.D.*

The radulae of four gasteropod species are here described and figured. Two species are from South Australia, and two from New Zealand. The new generic name *Austrancilla* is proposed for *Baryspira edithae* (Pritchard and Catliff) in which the opercular nucleus is situated on the pointed lower end of the operculum, and the shell is maculate. In radular formula *Austrancilla edithae* stands near *Baryspira*, but in the nature of the operculum it resembles *Turrancilla*.

1. *Anisodiloma lugubris* (Gmelin). Text fig. 1. The shell of this species has not a distinct tooth on the columellar margin of its aperture, but the radula shows close relationships with the *Monodonta* group in having the quadrate central tooth with a broad frontal margin and a large membrane on each side. This is the type species of the New Zealand genus *Anisodiloma* Finlay.

2. *Micrelenchus dilatatus* (Sowerby). Text fig. 4. The central tooth is rather narrow, and has a broad membrane on each side. This feature indicates that the genus is one of the *Cantharidus* group. This is also a New Zealand shell.

* Kyushu, Japan.

3. *Micrastraea aurea* (Jonas). Text fig. 2. The radula of this Australian species is close to that of the *Astraea* group, with a broad central tooth and four elongated lateral teeth.

4. *Austrancilla edithae* (Pritchard and Gatliff), *gen. nov.* Text fig. 3. This is a small ancillid species from South Australia, and is generally referred to the genus *Baryspira* with several other Australian species. The radula of this species is quite comparable with those of Japanese baryspirids, but differs from them in the operculum, the nucleus of which is situated at the pointed lower end. Moreover, the shell is slender and maculate. This species is therefore not referable to *Baryspira*, so the new generic name *Austrancilla* is proposed with this interesting species as type.



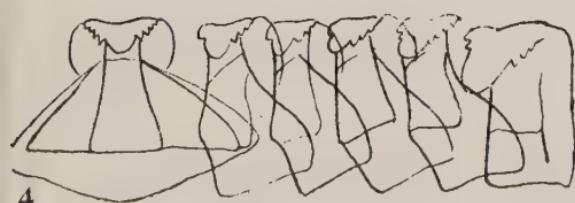
1. Central and five lateral teeth of *Anisodiloma lugubris* (Gmelin), from New Zealand.



2. Central, four lateral, and first marginal teeth of *Micrastraea aurea* (Jonas) from South Australia.



3. Central and marginal teeth of *Austrancilla edithae* (Pritchard and Gatliff) *gen. nov.* from South Australia.



4. Central and five lateral teeth of *Micrelenchus dilatatus* (Sowerby), from New Zealand.

AN INTERPRETATION OF THE MOLLUSCAN GENUS AMPHIDESMA IN NEW ZEALAND

By ELLIOT W. DAWSON.*

(Plate 4, text fig. 1-2.)

SUMMARY.

Amphidesma, a genus of heterodont bivalve molluscs belonging to the Mactracea, is characteristic of the sandy beaches of New Zealand; it occurs in a similar habitat in Australia, Chile, Argentina, Brazil, and in a number of places in the Northern Hemisphere.

A history of the nomenclature of these molluscs, variously described as *Amphidesma* Lamarck, 1818, or as *Mesodesma* Deshayes, 1832, is given; it is concluded that *Donacilla*, based on De Blainville's publication of Lamarck's informal name of "Donacille," is the correct name to be used for this group of molluscs. The name *Amphidesma* (although a subjective synonym of *Semele* Schumacher, 1817) is being retained only for the purposes of the present paper.

A consideration of speciation within *Amphidesma* in New Zealand, from a morphometrical study of some 35,000 specimens, shows that a cline exists from northern New Zealand to the south with a gradual lessening in height to length ratios, and increase in length of posterior end to height and to length ratios with higher latitude. The ends of the cline are marked by the "typical" *A. subtriangulatum* and *A. forsterianum* in the north and south respectively. The cline is not simple since intermediate forms may be found in many otherwise uniform populations especially in the middle region of the cline embracing the southern part of the North Island and the northern part of the South Island, and also at the Chatham Islands. The development of these forms is correlated with events in the late Tertiary and early Pleistocene, especially with the influence of the warm East Australian Current, allowing immigration of the Peronian fauna to New Zealand and with the retreat and advance of Subantarctic waters over New Zealand in the late Pliocene.

The development of *Amphidesma* has been correlated with the marine biotic provinces of New Zealand. The north end-point of the cline is the "typical" *Amphidesma subtriangulatum* in the hydrologically stable subtropical Aupourian Province and the southern end-point with "typical" *A. forsterianum* in the hydrologically stable subantarctic Forsterian Province. The intermediate populations of mid-New Zealand and the Chatham Islands, showing great variability, lie in the hydrologically unstable Cookian and Moriorian Provinces where factors of larval dispersal have been so variable that the present populations clearly reflect these environmental conditions.

Three species of *Amphidesma* are found in New Zealand. *A. australe* (easily separable subgenerically as *Paphies*) and *A. ventricosum*, the Toheroa of commerce are both quite distinct. The third "species" is composed of a complex or group of populations regarded as variants of a polytypic species with the clearly marked end-points to which the names *A.*

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subtriangulatum and *A. forsterianum* have been applied. The use of non-Linnaean "neutral terms" for informally describing these units is proposed.

The present account is offered as a preliminary to a major definitive revision of this genus now being undertaken.

INTRODUCTION.

For a number of years it has been common practice to use the name *Amphidesma* to denote a genus of bivalve molluscs characteristic of many of the sandy beaches of Australia and New Zealand, and it is, indeed, the dominant mollusc of this particular habitat in New Zealand. These bivalves, belonging to the Order Heterodontia and preferably included in the Mactracea (although some authors place them among the Tellinacea), also occur on the coasts of Chile, Argentina, and Brazil, as well as some parts of the Northern Hemisphere, where, however, they do not appear to be so dominant on the sandy shore.

Powell's "Check List of the New Zealand Recent Mollusca" (various eds., 1937, 1946, 1957) uses the generic name of *Amphidesma*, and all recent discussions of these molluscs in New Zealand (e.g.) Fleming, 1951 b; Rapson, 1952, 1954; Cassie, 1951, 1955; Pilgrim, 1954 a, b; Owen, 1958; Morton, 1958) followed Powell's lead. In fact, after the discussions of this genus by Iredale (1915) and by Finlay (1927), the alternative name for the genus, that of "Mesodesma," has not, despite Von Ihering's (1927) attempt to do so, been used in New Zealand since the time of Suter's "Manual" (1913), although many overseas workers have tended to favour it (e.g., Prashad, 1932; Coen, 1933; Thiele, 1935; Viader, 1937; Gardner, 1943; Habe, 1952; Abbott, 1955; Soot-Ryen, 1959).

In Australia, *Amphidesma* seems to have been used for a long time by various authors for the faunas of all coastlines from Western Australia to the eastern States (Hedley, 1916, 1917, 1918), not only in systematic studies (Cotton and Godfrey, 1938), but also in recent distributional and ecological work (Kershaw, 1958; Stephenson, *et al.*, 1958).

Finlay's (1927) decision "to obviate further error" in identifying the species of *Amphidesma* and his acceptance of this generic name seem to have been taken as the "last word" by subsequent workers. But this use has not always found acceptance either in other works or in other parts of the world.

There is, and always has been, a great interest in the largest species in New Zealand, *Amphidesma ventricosum* (Gray, 1843), known as the Toheroa, which is marketed as a commercial product. The recently published work of Rapson and of Cassie has revealed something of the biology of this species which appears, both by morphology and by distribution, to be quite distinct to the malacologist. However, the other species found in New Zealand have been by no means always easy to identify, and this is one reason why the literature has become encumbered with various names of doubtful status and with various remarks of doubtful significance.

A study of the biology of the common species of *Amphidesma* living on the sandy shores of Pegasus Bay, on the South Island of New Zealand, was begun some years ago (Dawson, 1954). It was found that, before any progress could be made on studies of growth, distributions and



A. forsterianum



A. australe



A. pliocenicum



A. ventricosum



Local *Amphidesma*



A. subtriangulatum

AMPHIDESMATIDAE



A. porrectum



Recent Chatham Is. Form

PLATE 4.

relationships, the Pegasus Bay species must be certainly identified. Even from a cursory glance it did not appear to fall directly into any of the existing named species, and, accordingly, as a necessary preliminary to the biological work, an investigation into the systematics of the genus *Amphidesma* in New Zealand had to be undertaken.

During this investigation, samples were collected from every possible part of New Zealand and from the Chatham Islands, and this material was supplemented by that already existing in various museum collections. In only certain restricted areas, such as parts of the coastline north of Auckland, where, in any case, only one "typical" form seemed to be present, were there any serious gaps in this coverage. In all about 35,000 specimens were handled during this work, and of these some 23,000 were measured in several ways for statistical analysis. It must be added that these figures, although of an order adequate to give a fairly true idea of the variability of the species concerned, are not so impressive as might appear when considered in relation to the size of the beach populations being sampled. For example, it was estimated that, during the 1953-54 summer, a 20-mile stretch of Pegasus Bay carried a population of some 1770 million individuals; this compares favourably with Coe's (1953) estimate for the smaller *Donax gouldi* of c. 677,600,000 individuals along a five-mile stretch of beach in California.

The purpose of the present paper is twofold. In the first place, I want to present a preliminary statement of the history of the names "*Amphidesma*" and "*Mesodesma*" as applied to certain bivalve molluscs in the Australian and New Zealand regions, and to offer the conclusion that the name *Donacilla* only should be used for these "donaciform" bivalves living in this area or elsewhere, pending further evidence to the contrary based on other interpretations of the rules for the selection of type species.

Secondly, it is thought that an outline of the systematic position of the species of *Amphidesma* in New Zealand, and of their relationships, might be of interest to Australian workers, based on my 1953-1954 survey and pending the appearance of a definitive major revision of this genus which I am attempting. The major gaps in this treatment are the lack of comparative Australian and South American material and the fact that examination of the New Zealand fossil *Amphidesma* has not been completed.

In addition to this, the present account may, perhaps, stimulate others, who may have been interested in this genus, to examine the forms occurring in their own areas.

1. STATUS OF THE NAME *AMPHIDESMA*.

In 1818, Lamarck founded the genus *Amphidesma* to include sixteen species from various parts of the world. In proposing this genus, he explained:

"Depuis assez long temps, j'avais établi ce genre dans mes cours, sous le nom de donacille (extrait du cours, etc., p. 107), parce que l'espèce que je connus d'abord avait l'aspect d'une donace" (Lamarck, 1818: 490).

Lamarck himself thought that *Amphidesma* was an artificial group, but that it seemed to be united by a number of common characters.

Immediately following Lamarck's work of 1818, confusion began. Sowerby (1820) figured Lamarck's first species, *Amphidesma variegata*, but preferred to group the genus closer to *Mactra*. Latreille (1825) placed *Amphidesma* in a family of its own, closer to *Lyonsia* rather than to *Mactra*, while, amongst other authors, De Blainville (1824) placed *Amphidesma* in the existing genus *Lucina* containing, as he put it, "espèces lenticulaires ou ovulaires."

Dubois (1824: 49), in a free translation of Lamarck's work, stated: "La Marck, on his first examination of the species of this genus, called it *Donacilla*, considering them to be allied to those of the *G. Donax*; but, on a subsequent investigation, he has determined to constitute the present genus of them, as they possess very peculiar characters, and are quite distinct from all other bivalves."

It was evident to Deshayes that certain of the species put into *Amphidesma* by Lamarck were allied not only to each other, but to some other Lamarckian species outside this genus. Hence, in 1832, he founded the new genus *Mesodesma*, to which he transferred three species of Lamarck's *Amphidesma* (*A. donacilla*, *A. cornea*, and *A. glabrella*), and also Lamarck's *Mactra donacia* and *Crassatella striata*. No type species was mentioned by Deshayes for Lamarck's *Amphidesma* or for his own *Mesodesma*, although his *M. donacium* has been generally taken as such by later workers. Following the practice of delimitation of genera so favoured in the nineteenth century, the remaining species of Lamarck's *Amphidesma* were similarly transferred to other genera.

Reeve (1853), in his monograph on *Amphidesma*, remarked:

"The genus as defined by Lamarck contained rather a miscellaneous assemblage of species. Some of these have been transferred to *Thracia*, some to *Mesodesma*, and some to *Syndesmya*, and several referred to this genus by Fleming and others have shared a similar fate. Of the Lamarckian species, *A. variegatum* (*Tellina obliqua*, Wood) may be regarded as the type of the genus as now constituted."

Lamy (1912 a: 159; 1914 a: 317) has outlined the fate of the sixteen Lamarckian species; briefly, five species now belong to *Scrobicularia* or to *Syndesmya*, three to *Mesodesma*, with one to each of the genera *Ervilia*, *Lyonsia*, *Thracia*, *Lucina*, *Thyasira*, *Lasaea*, and *Kellia*. In this way the genus *Amphidesma* has become an "empty shell." Nevertheless, the two generic names have been used and misused a great deal not only since the decision of Deshayes in 1832, but even since Lamy's reviews of the Lamarckian genera in 1912 and 1914.

Simply, the name *Amphidesma* seems to have been used for oblong, circular, or oval shells resembling *Semele* or *Syndesmya* or *Thracia* in appearance, while *Mesodesma* has, until quite recently, generally been applied to triangular or triangularly-ovate shells superficially resembling *Donax* or *Mactra*. Few workers have taken the trouble to look inside the shells and note details of ligament disposition, hinge and teeth as carefully as did Lamy in his studies of 1912 and 1914, and, hence, the names have often been used for quite superficial resemblances according to the whims of various writers.

We need not concern ourselves here with all the details and complications of the various species involved. Lamy's great reviews of the *Scrobiculariidae*, including *Amphidesma*, and of the *Mesodesmatidae* can

be consulted by those interested in this aspect. But we can at once proceed to the basic question. What is the type species of *Amphidesma*?

Lamy (1912, 1914), with access to Lamarck's original material, decided in favour of his first listed species *A. variegatum*, and followed Deshayes in his use of the name *Mesodesma*. However, Iredale (1915), considering the same question at about the same time, selected, "by tautonymy," *A. donacilla*, the second listed species of Lamarck, and resurrected his genus *Amphidesma* for the benefit of conchologists in New Zealand and Australia. We may re-examine these choices now.

If the type species of *Amphidesma* should be found to be a "semeliform" shell, *Mesodesma* would be available as a later name for certain allied "donaciform" or "mactroid" molluscs regrouped and removed from the original genus by Deshayes in 1832. The "elimination" of this genus *Amphidesma* is, of course, quite contrary to modern taxonomic practice, since some consideration must be made of type species. In selecting the type species of *Amphidesma* by subsequent designation, we must accept the earliest type-designation, that of J. G. Children (1823: 301) who selected *A. variegata* Lamarck. This species, the first member of the genus listed by Lamarck, has been considered by several subsequent workers to belong to the genus *Semele* as *Semele purpurascens* (Gmelin, 1792), according to Lamy (1914 a:350), and listed earlier as *Tellina* or *Semele obliqua* (Wood, 1815) by Dall (1886:279) amongst others. Although it seems obvious that Lamarck founded his new genus on a specimen reminiscent of the genus *Donax* in shape and that he put forward the name *Amphidesma* as a proper substitute for the vernacular "donacille," there seems to be little doubt that *Amphidesma* must be based on a "semeliform" rather than a "donaciform" animal other characters as portrayed by Lamarck being equal. Sowerby's (1820) figure of *A. variegatum* certainly indicates a "semeliform" species.

Since *Amphidesma*, based on a semeliform animal, is considered a subjective synonym of *Semele*, the "donaciform" members of the genus, separated by Deshayes, can now bear the name "*Mesodesma*." However, the name *Donacilla*, the Latinised version of Lamarck's "donacille" of 1812 has priority since it was first published, as Iredale (1915:490) has already shown, by De Blainville (1819:428):

"DONACILLE, *Donacilla*. (Conchyl.) M. de Lamarck, dans l'extrait de son cours, etc., page 107, avait donné ce nom de genre à une coquille bivalve, ayant l'aspect d'une donace, qu'il a fait entrer depuis dans le genre qu'il a nommé *Amphidesme*. Hist. nat. des anim. sans vert., 2^e édit., t. 5, p. 489 (De B.)."

Dr. L. R. Cox, F.R.S., has kindly drawn my attention to this question of priority, and has given me his opinion on the procedure necessary, and I am accordingly greatly indebted to him.

It seems that *Donacilla* must be treated as a generic name published with an indication but without an included nominal species, so that the first nominal species included in *Donacilla* becomes its type. The first author to adopt the generic name *Donacilla* Lamarck and to associate a nominal species with it was R. A. Philippi (1836:37, see also 1853:305, 311), who described a new species as *Donacilla lamarckii* and placed in its synonymy *Mactra cornuta* Poli and *Amphidesma donacilla* Lamarck. This enables the adoption of the generic name *Donacilla* for the "donaciform"

members of "Amphidesma" and for those of Lamarck's genera which were removed to "Mesodesma" by Deshayes. If "Mactra donacia Lamarck," the type of *Mesodesma*, is considered as congeneric with the type species of *Donacilla*, i.e., *Amphidesma donacilla*, then only *Donacilla* is available for this group, and, in any case, it must be considered as validly published prior to *Mesodesma*. A fuller treatment of this particular section of the present paper is being offered elsewhere (Dawson, 1959).

2. THE NEW ZEALAND SPECIES OF AMPHIDESMA.

Iredale (1915) has, in detail, set out the history of early changes in the nomenclature of *Amphidesma*, and this account is expanded and criticised by Finlay (1927). Oliver's work (1923) was apparently lightly dismissed by Finlay, but, as may appear from the present study, it is possibly the closest and most clearly outlined description of the status of this genus in New Zealand.

It is not necessary here to quote extensive synonymy nor to delve deeply into the history of the genus, but the salient features may be mentioned. Deshayes (1832) had included the following presumed New Zealand species in his genus *Mesodesma*: *M. donacium* ex Lamarck, *M. quoyi* sp. nov. and *M. gaymardi* sp. nov. Dall (1895; 1898) divided "*Mesodesma*" into the subgenera *Mesodesma*, *Donacilla*, *Taria* and *Paphies*, and Suter (1913) in his great "Manual of New Zealand Mollusca" followed Dall's usage and listed the New Zealand species thus: *Mesodesma (Donacilla) subtriangulatum* (Gray, 1825), *M. (Taria) ventricosum* Gray, 1843, and *M. (Paphies) australis* (Gmelin, 1791). A key to these subgenera was also given by Suter.

Iredale's (1915) interpretation of the New Zealand species was: *Amphidesma (Taria) gaymardi* (Deshayes, 1832), *A. (Taria) quoyi* (Deshayes, 1832), *A. (Taria) ventricosum* (Gray, 1843), and *A. (Paphies) australis* (Gmelin, 1791). Looking further into the species listed by Iredale, we find that, for a number of reasons, he regarded *A. gaymardi* as the name to be used for the species included by Suter as *M. subtriangulatum* (Gray, 1825). Iredale associated this species and *A. ventricosum* in the subgenus *Taria*, as there did not appear to be much superficial distinction, and he noted that the pallial sinus was small in both *A. gaymardi* and *A. quoyi*, but deep in *A. ventricosum*. Iredale considered that Suter had confused *A. quoyi* in his description of *M. ventricosum*. Furthermore, Iredale distinguished *A. quoyi* from *A. ventricosum* in the following points: "A. *ventricosum* Gray is longer and narrower than *A. quoyi* Deshayes, and approaches *A. gaimardi* [sic] in shape. *A. quoyi* has the posterior slope flattened, while in *A. ventricosum* the posterior slope is bicarinate. In *A. quoyi* Deshayes the siphonal inflection is not deep whilst in *A. ventricosum* Gray it is very deep." Suter, in his description of *M. ventricosum*, stated that the pallial sinus is horizontal with a circular anterior end reaching not quite the middle of the shell, and he made no mention of a bicarinate posterior end. However, in his description of the subgenus *Taria*, in which he placed *M. ventricosum*, he noted: "pallial sinus well marked, sometimes deep." Hence, both of Iredale's species *A. quoyi* and *A. ventricosum* could be included in this subgenus *Taria*.

Oliver (1923) discussed the nature of *A. subtriangulatum*, and his remarks, as earlier mentioned, are worthy of some attention. He said of this species: "This appears to be a variable species, the extreme forms of which are the thick, angled, triangular form from the North, and the flattened, more ovate, form from Banks Peninsula and other localities to the South." He pointed out that, contrary to Iredale's notions, Suter had not confused *A. quoyi*, which was represented by these southern more ovate shells, with *A. ventricosum*, but had included it in his description of *A. subtriangulatum* by the use of a series probably greater than was available to Iredale. Oliver continued, interestingly, thus:

"That we are dealing with one variable species, and not two species, is shown by the fact that variations in those characters which are supposed to separate *quoyi* from *subtriangulata* may be observed in the same locality. For instance, in shells from the Chatham Islands the angle formed by the dorsal and posterior side varies through several degrees, while shells from Takapuna vary in the thickness of the shell. While it is thus not practicable to separate a long series of shells from many localities into two species, yet those from the north-east coast between Spirits Bay and Tauranga are usually heavy ventricose shells with the posterior end short and, therefore, the angle made by the dorsal and posterior sides comparatively small. Shells from Kaipara and Gisborne southwards, and from the Chatham Islands, are almost invariably of the broad-angled, thin form. If it be convenient to refer to these differences *subtriangulata* and *quoyi* might be used subspecifically, but in this case *quoyi* would not have the meaning intended by Iredale, but include besides the greater part, so far as area of distribution goes, of the species *subtriangulata*."

Finlay (1927) attempted to end all confusion as to the species of *Amphidesma* in New Zealand. He began his criticisms by stating that Oliver's notes needed some revision since he had confounded distinct species. Oliver had, according to Finlay, misinterpreted Iredale's comments on Suter's identification of *M. quoyi* with *M. ventricosum*, and Finlay emphasised Suter's use of the expression "pallial sinus well marked, sometimes deep" in his description of the subgenus *Taria*. Finlay stated that the pallial sinus in true *ventricosum* is always deep and "so that only one conclusion is possible to account for the use of the word 'sometimes,'" and that is that a species with a short pallial sinus had also been examined." However, one may now note that, in Suter's key to subgenera, *Taria* is characterised by the possession of a pallial sinus "reaching to near the centre" and, therefore, Oliver's suggestions, based on Suter's actual specimens and on Suter's inclusion of *M. lata* as a synonym, that *quoyi* was included by Suter in his *M. subtriangulatum* are apparently substantiated. Finlay further pointed out that one cannot adopt Oliver's suggestion of using the names "*quoyi*" and "*gaymardi*" subspecifically since both these names, and *subtriangulatum*, were given to the northern forms as is shown from a study of such published figures as are available. Finlay found, therefore, that the southern, more ovate, form was nameless, a point which concerns the species from Pegasus Bay which forms the basis of the present study. The confusion, he suggested, was due to the fact that there are two bicarinate species, *i.e.*, *subtriangulatum* is bicarinate as well as *ventricosum*, whereas the southern shell is smooth, having no carinae on the posterior margin. Finlay's conclusion was that ". . . we can now understand how *subtriangulatum* was sometimes lumped with

the southern shell (on account of its shape and sinus), and sometimes, by Suter, with *ventricosa* (on account of its two carinae) . . .”

Finally, Finlay proposed the name “*Amphidesma forsteriana*” for this southern species. The key he gave, which implied the “last word” on the *Amphidesma* question, is given again here:

“Shell inequilateral

Adult shell posteriorly bicarinate.

Pallial sinus deep *ventricosa*

Pallial sinus shallow *subtriangulata*

Adult shell posteriorly unicarinate, sinus shallow.

Shell very high and crass, posterior dorsal area cut straight
in *crassiformis*

Shell high but not crass, posterior dorsal area moderately
cut in *pliocenica*

Shell neither high nor crass, posterior dorsal area rather
expanded *forsteriana* n. sp.

Shell subequilateral, not carinated *australis.*”

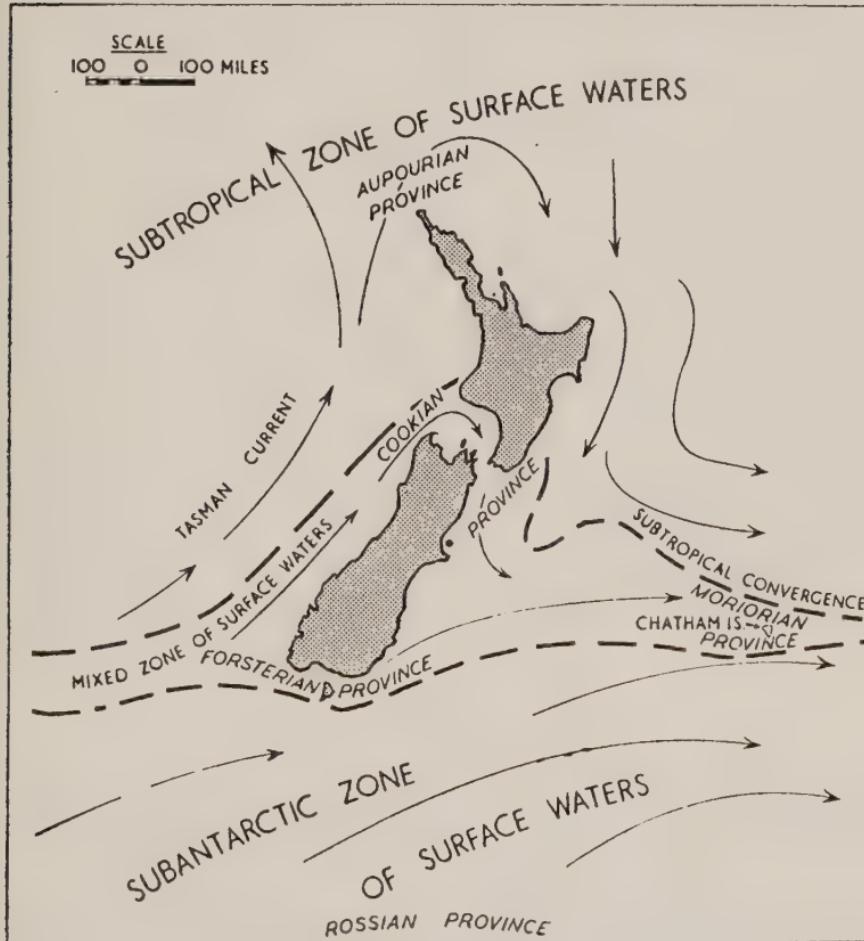
This key, since it represents the latest opinion on the New Zealand species, may be taken as the starting point for the present inquiry.

The *Amphidesma* in Pegasus Bay, the Banks Peninsula populations and those from Otago beaches all seem to fall into Finlay's *A. forsterianum* which he characterised as having an “inequilateral rather small shell not high nor crass, nor inflated; rather short anterior end in comparison with *subtriangulata*, and more produced posterior end, the beaks being therefore much less posterior; wing-like expanded posterior dorsal area, not sharply cut in, and with no distinct second medial carination, the bordering main carination being itself weak; and short pallial sinus.”

On passing up the South Island into the Cook Strait region and along the Wellington coasts, we find shells appearing with characters of shape between the two extremes of *A. subtriangulatum* (= “*subtriangulata*” of Oliver) and *A. forsterianum* (= “*quoyi*” of Oliver). The Toheroa, *A. ventricosum*, is a distinct enough form although the representatives from the Southland beaches appear to be more truncated anteriorly and may, as Finlay suggested, deserve taxonomic recognition. The very small individuals of *A. ventricosum* and *A. subtriangulatum* are often rather difficult to distinguish in the field. On the Chatham Islands, 500 miles to the east of Banks Peninsula, shells occur which seem to have what might be called “*subtriangulatum* tendencies,” although others appear to belong to *A. forsterianum* with populations resembling the fossil form *A. porrectum*. It is of interest, in this connection, to note Finlay's (1928: 280) remarks: “It would be very interesting if the broad, triangularly ovate, unicarinate *forsteriana* Finlay were to occur at the Chathams also, as this would prove the two forms absolutely distinct, instead of only regional relatives. Till evidence is forthcoming, however, it seems best to admit only *subtriangulata* to the Chathams fauna.” A second quite distinct medial carination has sometimes been seen in “typical” *A. forsterianum* from Banks Peninsula and Otago, and in many others the bordering main carination of the posterior dorsal area is quite angled. The pallial sinus in both northern and southern forms appears similar in

size, shape and position, although individual variation exists, as may be seen by glancing at the shells forming any single natural population.

Lack of precision of the delimitation of the various forms is such that both the figure of *A. subtriangulatum* given by Suter (1915, pl. 59, fig. 19) and by Powell (1937, pl. 11, fig. 7) may be taken as representing



Text Fig. 1.

examples of the intermediate forms rather than the "typical" forms. However, Moss (1908, pl. 8, fig. 24) illustrated, under the name of *Atactodea subtriangulata*, a "typical" example of *A. subtriangulatum*. Bucknill's figure (1924, pl. 17, fig. 13) illustrates a shell close to the "typical" *subtriangulatum*. Indeed, Powell's figure could well illustrate some of the Chatham Island shells, in particular specimens which I collected in 1954 from Ko-ro-Kopuroa, near Owenga.

Of extinct species of *Amphidesma*, several have been collected in New Zealand. *A. crassiforme*, described by Marshall and Murdoch (1920) on three valves from blue sandy clay at Nukumaru (lower Pleistocene), was "distinguished by its massiveness and abrupt heavy truncation." *A. porrectum*, described by Marwick (1928) from mid to upper Pliocene soft Bryozoan limestone at Titirangi, Chatham Islands, was "distinguished from *A. subtriangulatum* by the greatly elongated anterior end, and the generally strongly convex posterior end, also the pallial sinus is deeper and the posterior muscle scar somewhat larger." Many further specimens of this form were collected in 1954 at the type locality for the present study. *A. subtriangulatum pliocenicum*, described by Oliver (1923: 187) from "the Pliocene beds at Castlecliff" (now regarded as Pleistocene), was distinguished by being "higher than either of the recent forms, and the angle of the dorsal and posterior sides is intermediate. It is more distinct from the two recent forms than they are from each other . . ." Oliver's last remark, as first pointed out by Finlay (1927), is belied by the fact that, in general, *pliocenicum* possesses no secondary carination, and it seems to be directly ancestral and quite close to *A. forsterianum*. Dell (1950) has described from a single valve an early *Amphidesma* from a Miocene bed at Waikiwhai, Auckland, as *A. (Paphies) anteaustrale*. Recent species occurring as fossils, distinguished earlier as separate species in many cases but now synonymised, have been listed by Hutton (1873, 1880), Suter (1910, 1918), and Thomson (1920), and Te Punga (1952). Finlay (1924) has listed from the Miocene of Awamoia a young shell considered to be "*Amphidesma subtriangulatum* Wood" found in very hard and rather poorly fossiliferous mudstones, now regarded as of upper Pliocene date. Finlay suggested that this shell might be "referable to the subsp. *pliocenica* Oliver." Apart from Dell's record of *Amphidesma (Paphies)* from the lower Miocene (Altonian), this may well be the earliest record of the genus in New Zealand if it is authentic. Dr. J. Marwick (pers. comm., 1953) has been unable to locate this specimen in the Geological Survey collections.

3. SPECIATION WITHIN AMPHIDESMA.

For the purposes of the present paper aspects of speciation and distribution of *Amphidesma* will be discussed only in general terms. Extensive data, in the form of specimens and measurements, is, however, available to substantiate statements which may be made here.

Amphidesma, although of little value to the palaeontologist concerned with happenings in the Tertiary, is a useful genus in two ways: it illustrates the variation that may occur within a single genus in recent times, and, secondly, it is a convenient model for demonstrating the status of the concept of marine biotic provinces within New Zealand.

The nature of "species" has been well dealt with on a number of occasions by Mayr (1942, 1948, 1957), and, for the palaeontologist, by Sylvester-Bradley and others (1956). Mayr has shown that, basically, there are only two species definitions: "morphological," based on the degree of difference, and "biological," based on the amount of gene interchange—in other words, on the degree of reproductive isolation. Mayr's (1942) definition of species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from

other such groups" may be commended as a simple expression based on the population, *i.e.*, on the smallest interbreeding unit.

It appears well founded, from earlier authors' conclusions and from a consideration of the present distribution of *Amphidesma*, that there are, in New Zealand, three living "species," *A. australis*, *A. ventricosum* and the *A. "subtriangulatum-forsterianum"* group. It is in the consideration of the extent and limits of this third "species" group that difficulties arise. It can be shown by examination of the ratios of length of posterior end to height (D/H) and of length of posterior end to total length (D/L) for populations of *Amphidesma* from throughout New Zealand that an apparent cline (see also, Clench, 1954) may exist in which there occurs a gradual morphometric character change with latitude. As *Amphidesma* progresses from northern New Zealand south towards Stewart Island, there is a gradual lessening of the height to length (H/L) ratio, an increase in D/H and D/L and, hence, a prolongation and expansion of the posterior end with higher latitude. The ends of the cline are marked by the "typical" *subtriangulatum* and *forsterianum* forms. This cline is not so simple, however, as it may appear. Intermediate forms may be found in many otherwise homogeneous populations. This is particularly so in the region embracing the southern part of the North Island and the northern part of the South Island and also at the Chatham Islands. Infraspecific categories have always proved a headache for taxonomists, both with recent (Mayr, 1942, 1957; Emerson, 1952), and with fossil material (Newell, 1947; Dawson, 1952; Sylvester-Bradley, *et al.*, 1956). Mayr (1942) defined the only recognised infraspecific category, the subspecies, thus: "Subspecies are geographically defined aggregates of local populations which differ taxonomically from other such subdivisions of a species." Subspecies must be considered, also, as an assemblage of local populations. Such populations are classified on these bases: geographical relationship, presence or absence of morphological difference, and of reproductive isolation.

Perhaps the populations of *Amphidesma* in the intermediate zone of this supposed cline might be thought of as marking the area of contact of two well-defined subspecies. The morphological characters of expansion of posterior end and, particularly, presence of carinae or rays do not seem to be strictly valid for designating each population, and almost every local group appears "different," so that shells may be referred to certain beaches merely by examination of the external morphology.

Despite this, instead of taking the "easy" way out and merely calling each "different" group a new species or subspecies, it seems possible to reconcile this variation with the late geological history of the New Zealand marine molluses. Fleming (1944) and Dell (1952) have outlined the general distribution of ocean currents in relation to New Zealand. Without going into details of the oceanography involved, it may be said that a warm current from eastern Australia, the "Notonectian Current" (= East Australian or Tasman Current) strikes New Zealand in the vicinity of South Westland and travels the length of the West Coast, joining up with other water movements from the South-west Pacific to form the East Cape Current, sometimes sweeping well down to Banks Peninsula or further south during the summer. On the other hand, the cold West Wind Drift, from the Subantarctic, also approaches the South Island, sweeping eastwards towards the Chatham

Islands. In this way, a zone of so-called "mixed" waters is formed. The boundary, approximate as it may be, between the "warm" and "cold" waters, is referred to as the Subtropical Convergence, and profound influences on faunal relations have been correlated with it.

The development of the New Zealand molluscan fauna seems to have been such that, as Fleming (1944, 1949, 1951 a) has shown, several trends may be noted: (1) the evolution of an "autochthonous" element, the ancestors of which were already on the New Zealand scene in early Tertiary or even late Cretaceous times, (2) the reinforcement of such fauna by Indo-Pacific and possibly other elements during the Tertiary, (3) the extinction of mid-Tertiary genera in the Miocene and early Pliocene, and (4) the sudden immigration of species of East Australian origin in the late Pliocene and early Pleistocene, which has continued in post-Pleistocene times.

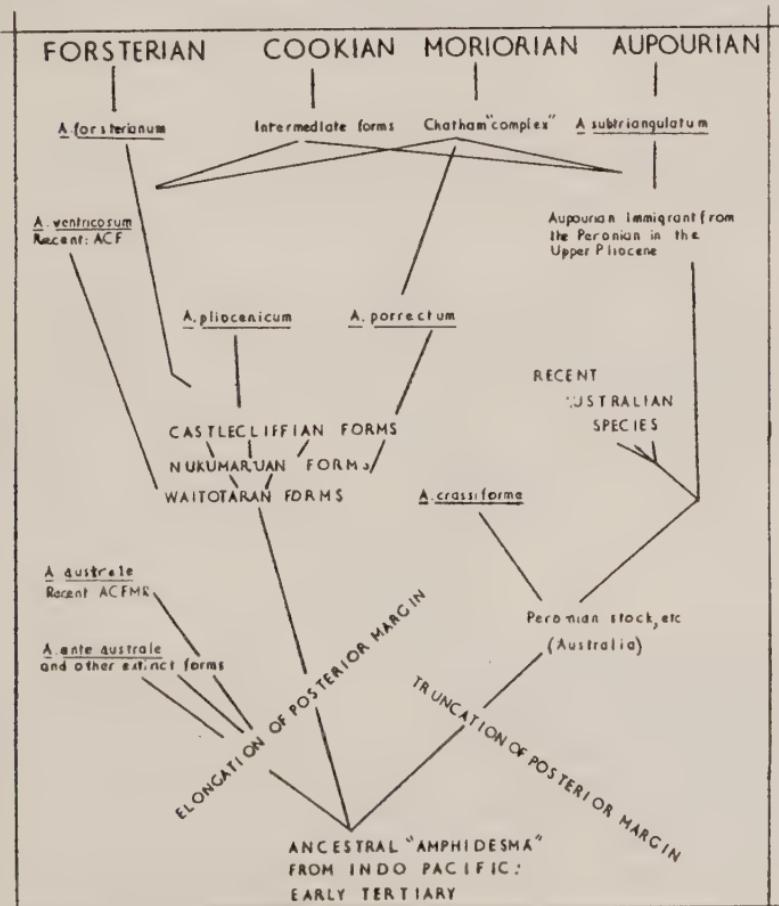
Amphidesma, in New Zealand, may be considered to appear in the Waitotaran Stage of the Upper Pliocene and in the Lower Nukumaruian Stage of the lower Pleistocene. Conditions, then, were such that there was a northward advance of cold water accompanied by migration of a number of genera of southern origin into what is now the middle of New Zealand. In this way, areas in North Canterbury, southern Hawke's Bay, and Wanganui, were affected by seas of the Subantarctic zone. In the Upper Nukumaruian, a retreat took place. *Amphidesma* may have become established in these times and some of the "odd" fossil forms, about which little data are available, may be correlated with happenings at this time. In the following stage of the Pleistocene, the Castlecliffian, the influence of the Tasman Current was felt, many genera from the east Australian sources now having suddenly appeared. This is, no doubt, when *Amphidesma*, as such, became an obvious faunal element, since additional stock may have been brought in from East Australia. The presence of the Tasman Current inhibited further advance of Subantarctic waters and prevented New Zealand seas from showing the further effects of cooling which culminated in the Pleistocene glaciation.

Amphidesma "forsterianum" may be considered the recent expression of late Pliocene stock. Nukumaruian specimens suggest that the ancestral *Amphidesma*, as indicated in *A. pliocenicum* of Oliver, was of a high H/L ratio with an elongated and expanded posterior end. The hypothesis is offered here that this group of forms, gradually evolving in early Pliocene times, retreated southwards with the Notonectian influence. The Castlecliffian immigration, with the new stock of *Amphidesma*, contributed further variation and, particularly in North Auckland, *Amphidesma* of another form, with a truncated posterior end and a more massive shell, occurred, perhaps as a direct result of the immigration of Peronian fauna from East Australia or as a descendant of the fossil *A. crassiforme*. It is further suggested that, in later time, the "*forsterianum*" stock gradually moved northwards again and the "*subtriangulatum*" or Peronian stock moved southwards, a trend which may well be continuing. In another connection, it has already been shown (Dawson, 1952) with reference to changing conditions in the New Zealand climate what rapid evolution may occur in small isolated communities. The limiting factor preventing further intermixing of surface waters and dispersal of larvae from various stocks may be principally one of temperature associated with general hydrology (cf. Fleming, 1952). At this point we may conclude this

account by associating developments within *Amphidesma* with present concepts of marine faunal provinces in New Zealand.

4. DISTRIBUTION OF AMPHIDESMA IN RELATION TO MARINE BIOTIC PROVINCES IN NEW ZEALAND.

The division of the New Zealand (or Maorian) sub-region into faunal provinces, a province being an area within a faunal region exhibiting a marked percentage of endemism, was the result of the efforts of Iredale, Finlay, and Powell. Hydrologically, the provinces may be delimited thus: AUPOURIAN—within the Subtropical zone of surface water—North Auckland peninsula and the Three Kings Islands from above Ahipara on the west Auckland coast and Whangaroa on the east coast; COOKIAN—mixed waters of the middle region of New Zealand—rest of the North Island and the northern part of the South Island south to Westport on the west coast and Banks Peninsula on the east coast; FORSTERIAN—isolation and predominant Subantarctic waters—Otago, Southland and Stewart Island; MORIORIAN—isolation and mixed waters—the Chatham Islands; ROSSIAN—completely within the Subantarctic zone of surface water, Subantarctic islands and seas.



Text Fig. 2.

The Aupourian province seems, indeed, to be the domain of the "typical" *Amphidesma subtriangulatum*, the northern end of the so-called cline. Almost all marine organisms found in this province are characteristic of Subtropical conditions, and hence *A. subtriangulatum* here may be stenozonal, being limited by temperature considerations. On the other hand, the Forsterian province is clearly defined for most molluscs as a predominantly Subantarctic zone and is none the less so for *Amphidesma*, this being the domain of the "typical" *A. forsterianum*.

The particularly interesting provinces, from the aspect of *Amphidesma* and the dispersal of its larvae, are the Cookian and the Moriorian. The Cookian, as indicated, is within a zone of relatively mixed waters. The fluctuation in position of the Subtropical Convergence, which may be considered its northern boundary, makes this zone hydrologically unstable and hence biologically variable. Hence it is not surprising that within this zone *Amphidesma* should show great variation. It is only from Westport, on the west coast of the South Island, and from Pegasus Bay, on the east coast, that *Amphidesma* appears morphometrically stable to the south. In the north, it seems that only from about Kawhia and Tauranga, on the west and east coasts, respectively, of the North Island, does this occur, although *Amphidesma* with "forsterian" affinities occurs even at Manukau Heads, near Auckland.

CONCLUSIONS.

It can be seen that *Amphidesma* is a highly variable genus in New Zealand, and some doubt may be expressed as to a suitable nomenclature for the various forms, along the lines proposed by Newell (1947) or by Emerson (1952).

Amphidesma subtriangulatum pliocenicum, so named by Oliver, appears close to the recent *A. forsterianum* of Finlay, and much more distantly related to the Aupourian "typical" *A. subtriangulatum*. Hence, it might be suggested that the fossil form be raised to specific rank and, thus, that *A. forsterianum* = *A. pliocenicum*. However, since *A. subtriangulatum*, *sensu stricto*, is not clearly separable from the Recent Cookian *Amphidesma*, then, perhaps, the wisest thought would be to regard all these forms as variants of a polytypic species:

Aupourian, *A. subtriangulatum subtriangulatum*;
Cookian, *A. subtriangulatum cookianum*;
Forsterian, *A. subtriangulatum pliocenicum*;
Moriorian, *A. subtriangulatum moriorium*.

Systematics, as such, is useful to the ecologist for practical purposes since it enables him to have a "label" by which to refer to the particular animals with which he is dealing. As his studies become more refined, a mere label is not enough, and he will need to know precisely with which animal he is dealing and something of its relationship to other similar animals. Within the gross limits of the working needs of marine ecologists in New Zealand the above scheme may be useful until the full details of the complexes and intermediate forms, such as occur in the Moriorian and Cookian provinces due to the interplay of larval dispersal and hydrology, are made clear.

Convenient expressions, known as "neutral terms," are available for informally describing taxonomic units of doubtful status. The terms

generally used are *form*, for a single unit, and *group* or *complex*, for a number of units. Hence, form may be used when it is not known whether the unit being considered is a full species, a subspecies of a polytypic species, or merely an individual variant. The taxonomic status of the molluscs belonging to the genus *Amphidesma* in New Zealand may be resolved in the following way: *A. ventricosum* is predominantly Aupourian, extending into the Cookian with a representative, possibly the mark of a relict fauna, in the Forsterian. *A. australe* (conveniently separated subgenerically as *Paphies*) is euryzonal, extending from the Aupourian to the Forsterian and Moriorian, with a representative in the Rossian (= Antipodean). In contrast to these relatively clearly defined species, there is what may be called the *Amphidesma subtriangulatum* Group or Complex. Since a non-Linnaean terminology is to be preferred, the varieties found in each marine province may be referred to as the Aupourian Form, the Cookian Form, and the Forsterian Form, with the mixed populations of the Chatham Islands, where the situation seems especially involved, known as the Moriorian Complex.

Finally, *Amphidesma*, as a taxonomic problem, has well illustrated the change in thought of systematists within the past fifty years from the "type" concept of the nineteenth century conchologist to the "population" concept of Mayr, Dobzhansky, Simpson, and Huxley. In New Zealand, and also in Australia, it appears that the "new" systematics is yet to fill its role fully, and, while agreeing with Dell (1953) that we must bewail the state of affairs that results from "a constant search for differences, forgetting the likenesses, from a desire to name all separable forms and from a lack of appreciation of the facts of geographical variation and isolation," it is felt that the further delimitation and intensive study of populations of such variable genera as *Amphidesma* will prove invaluable in putting molluscan systematics in New Zealand, and in Australia, on a sound basis. Apart from this, it is suggested, based on the idea expressed in Occam's Razor that hypotheses should not be unnecessarily increased in number and should be phrased in the simplest possible way, that to call a "different" form a *new* species is, in these days of enlightened taxonomic thought, not sufficient, and evidence must be brought forward to show how otherwise it could not be fitted into the existing framework of that particular genus or unit.

I should like to conclude by expressing my appreciation of the guidance and friendship of the late Professor E. Percival, F.R.S.N.Z., University of Canterbury, New Zealand.

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LONG TERM CHANGES IN INTERTIDAL ZONATION IN TASMANIA WITH SPECIAL REFERENCE TO THE MOLLUSCA

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(Plates 2-3; text fig. 1.)

Abstract.

A study carried out over eleven years of the intertidal zonation in Tasmania shows certain changes which take place over a long period of time. These changes affect many groups of organisms, but the most serious effect is upon the Mollusca, so that lists of molluscan species of an area can vary greatly from year to year. Interspecific competition is important in long term changes.

Introduction.

The usual method of studying the intertidal zonation is for several visits to be made to one area over a short period of time and the results then written up. In many cases the area is then abandoned completely or else visited sporadically. The present paper is based upon the results of regular visits to four localities over a period of eleven years. On each visit the shore was examined in some detail and major changes in zonation were noted. Each locality was visited once per annum at approximately the same time of the year, and some places were visited more frequently. Certain algae which are known to fluctuate seasonally in density on the shore are not included in this study. These are *Ulva lactuca* (L.), *Colpomenia sinuosa* (Roth.) Derby & Sol. and *Scytoniphon lomentarius* (Lyng.) Ag.

The ecological nomenclature used is that of Stephenson & Stephenson (1949), and the author of each species is only cited once.

It is essential to state that the phenomena recorded below have been noted on shores of a low tidal amplitude, about 2' annual average tides with a maximum of 5' at springs. Further, all the localities concerned suffer moderate to low wave action. The latter type of coast was selected because the fauna of coasts suffering intense wave action is liable to be severely altered by gales. Although such changes may be widespread, it is other longer period changes which are the subject of the present study.

Specific Examples of Changes.

The four localities at which regular visits were made are Dodge's Ferry, Coles Bay, Fisher Island and Blackman's Bay (text fig. 1). The results obtained at these places have been confirmed by examinations of the shore at other localities.

(1) Dodge's Ferry.

Dodge's Ferry is situated on a sheltered coast in southern Tasmania. One of the features of the shore in December, 1949, was the very well developed belt formed by the serpulid worm, *Galeolaria caespitosa* (Lam.). This species, of encrusting habit, formed a massive belt up to 5" in thickness on the rocks. The spaces below and around the worm tubes

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Text Fig. 1.

were inhabited by a numerous fauna consisting of *Kellia australis* (Lam.), *Mytilus planulatus* (Lam.), *Austromytilus rostratus* (Dunker), *Lepisithais vinosa* (Lam.), *L. reticulata* (Blainv.), *Sypharochiton maugaeanus* Iredale & May, polynoid, phyllodocid and nereid worms and the anemone *Actinia tenebrosa* (Farq.). The molluscs may be considered as characteristic of the fauna to be expected on this part of the shore.

During the year 1950 the tube masses broke away from the rock, and instead of the thick belt of *Galeolaria* there remained only a thin scattered layer of tubes. Since 1950, there has been a slow colonization of the shore by *Galeolaria* with the result that the tubes now form a more or less continuous sheet on the rocks at the appropriate tidal level. However, there is not yet any development of the thick masses of worm tubes. Living amongst the *Galeolaria* tubes in March, 1958, and utilizing the rock as a substratum was a numerous fauna consisting of *Cominella lineolata* (Lam.), the buccinids *Lepisithais reticulata* (Blainville) and *L. vinosa*, the chitons *Poneroplax albida* (Blainville) and *Sypharochiton maugaeanus* Iredale & May, the limpets *Patelloida alticostata* and *Chiazacmea flammnea* (Quoy & Gaim.), the siphonarians *S. diemenensis*, *S. funiculata* and *S. tasmanica*, the nassariid *Tavaniota tasmanica* (Ten-Woods) and the thaid *Agnewia tritoniformis*.

Certain of these species are not usually associated with *Galeolaria* masses. *Poneroplax albida* generally is considered an inhabitant of the Infralittoral fringe, but is sometimes found at higher shore levels. The feeding habit of this chiton, together with its large size, prevents it from living amongst the fully developed *Galeolaria* masses. The limpets,

P. alticostata and *C. flammæa*, as well as the three species of *Siphonaria* and *Tavaniøtha tasmanica* also are not usually found in the *Galeolaria* belt.

In addition to the appearance of the above species, *Kellia australis* had disappeared from the tidal levels at which it was previously found. This lamellibranch requires small spaces in which to live, and this environment is usually supplied by *Galeolaria* tubes, seaweed holdfasts or by the coralline alga *Lithophyllum hypercellum* (Foslie).

In 1949, the *Galeolaria* masses were replaced at lower tidal levels by beds of *Mytilus planulatus* (Lam.), which in turn were replaced by the ascidian *Pyura stolonifera* (Heller). In 1956 the mussel beds were almost non-existent, the mussels being confined to the lower part of the *Galeolaria* belt, which extended as far as the *Pyura* belt (Plates 2 and 3). The *Pyura* belt had extended up the shore to meet *Galeolaria*, and the belt was more densely populated by ascidians.

The removal of the mussels was not caused by a gale, since the region where the beds were found is in a sheltered locality where strong enough seas for this purpose could not arise. The cause of the disappearance is not known. However, the effect upon the fauna is very great. The mussels, which were packed closely together, furnished a sheltered habitat for many species. The most common of these were *Cominella lineolata*, *Patelloidea alticostata*, *Notoacmea corrosa* Oliver, *Venerupis dizmenensis* Q. & G., *Kellia australis* (in byssus strands), *Ostrea virescens* Angas, *Hiatella australis* (Lam.), the crabs *Helice haswellianus* Whitelegge, *Petrolisthes elongatus* M. Edwards, *Halicarcinus ovatus* (Stimpson), numerous worms, amphipods and isopods, as well as algae such as *Ulva lactuca* L. *Polysiphonia* spp., *Laurencia botryoides* (Gaill.) and *Gigartina* sp. The barnacles *Chamaesipho columna* (Spengler) and *Chthamalus antennatus* (Darwin) lived attached to the shells of the mussels.

Consequent upon the disappearance of the mussels, the great majority of this fauna disappeared from the appropriate shore level. The only species still to be found were *Patelloidea alticostata*, *Helice haswellianus*, and the two species of barnacles together with a few *Mytilus planulatus*, which remained either as isolated individuals or as scattered small clusters.

The recolonization of a denuded area by *Mytilus* usually starts soon after the clearing of the rocks. It was noticed at Blackman's Bay that rocks which were covered by *Mytilus* beds were very rapidly recolonized by mussels after they had been denuded by a storm (Guiler, 1954). The same process started less rapidly at Dodge's Ferry, but it has now reached a stage where mussels are common on the rocks.

The upward spread of the ascidian *Pyura stolonifera* (Heller) has already been noted. This species furnishes a habitat which is suited to some species of mollusc, notably *Acanthochiton sueurii* (Blainville), *Sypharochiton maugeanensis*, *Amaurochiton glaucus* (Gray), *Patelloidea alticostata* (Angas), *Cominella lineolata*, *Kellia australis*, *Venerupis exotica* (Lam.), *Dentimitrella lincolnensis* (Reeve), *Dicathais orbita* (Gmelin). Other species found are the echinoderms *Helicidaris erythrogramma* (Val.), *Uniophora sinusoidea* (Perrier), *Coscinasterias calamaria* and *Tosia aurata* (Gray), the crustaceans *Halicarcinus ovatus* (Stimpson), *Petrolisthes elongatus*, and the sponges *Hymeniacidon perlevis* (Montagu) and *Tethya diplodera* (Schmidt).

(2) Coles Bay.

I have already drawn attention to the change in zonation at Coles Bay (Guiler, 1953). It was found in 1950 that *Mytilus planulatus* and the alga *Hormosira banksii* (Turn.) Decaisne were in very intense inter-specific competition. In 1956, it was found that *Hormosira* has become more numerous and was dominant over the mussels, particularly at localities known as Honeymoon Beaches. The same situation is true at the present time. However, at the Fisheries, both in 1956 and 1958, the reverse held true, *Mytilus* having achieved dominance. These results suggest that there may be frequent changes in dominance between these two species in this area.

The *Galeolaria* belt, which was very well developed in 1950 and virtually absent in 1953, has not yet regained a place of ecological importance on the shore.

The belt formed by *Austromytilus rostratus*, but poorly developed in 1950, had extended by 1953, and by 1958 was a very prominent feature of the shore. This mussel does not have as many species associated with it as *Mytilus*, and being a smaller mussel, does not offer such an extensive habitat between the mussels and the substratum.

(3) Fisher Island.

This island is situated near the southern end of Flinders Island in Bass Strait, and is the site of a small Biological Station. The island was first visited in March, 1954, and subsequently in November, 1956, and February and March, 1957. During this period the most significant change has been the development of a *Hormosira* belt in the Midlittoral at the southern end of the island. In 1954, *Hormosira* was linked with *Galeolaria* as forming a joint belt on the eastern shore of the island, but since then it has spread to such an extent that it forms a band all around the island at the bottom of the *Galeolaria* belt. Correlated with the appearance of the *Hormosira*, there is an apparent lessening in the width of the *Galeolaria* belt. However, the tubes of *Galeolaria* still exist, and are occupied by worms, on the rocks among the *Hormosira* plants. There is no evidence that in recent years *Galeolaria* has formed a thick encrustation on the shores of Fisher Island, though there was a thick encrustation on sheltered parts of the island in 1957 (Guiler, Serventy and Willis, 1958). However, the typical fauna of the *Galeolaria* belt was poorly developed.

Modiolus pulex Lam. is of some local importance on Fisher Island, and supports a varied fauna consisting of *Cominella lineolata*, *Lepisithais vinosa*, *Hipponix conicus* (Schumacher), *Melanerita melanotragus*, *Micrasstraea aurea* Jonas, *Serpulorbis siphon* (Lam.), *Fax tenuicostata* (Ten. Woods), *Sypharochiton maugeanus* and *Cryptoplax iredalei* (Ashby). The region where these mussels occur is sheltered from the waves, and has been occupied by mussels for a number of years.

Another change noted was the density of barnacle population. In 1954 there were not many barnacles on the island, but it was noted that there had been widespread and apparently successful spatfall in that year. This spatfall continued to survive, as is witnessed by the large number of *Chamaesipho* of uniform size on the shores of the island.

(4) Blackman's Bay.

A most interesting change has occurred in this area, where the limpets *Cellana solida* (Philippi) have become exceedingly rare or absent over much of the lower part of the Derwent estuary. In 1950, I described *Cellana* as occurring commonly at Blackman's Bay, especially on the platform at the northern end of the Bay. Examinations carried out in 1957 by myself and Dudgeon (*in litt.*) show that this limpet has become scarce over a considerable part of this coast. The reduction in the number of limpets has resulted in the virtual elimination of the Patelloid belt described earlier (Guiler, 1950). The band has been replaced by downward extension of the *Galeolaria* belt and partly by an upward extension of the *Austromytilus rostratus* belt.

Discussion.

The changes recorded above are all concerned with species which are known not to suffer large annual variations in population density. All of the species are of importance on the shore since they are concerned with the formation of belts of zonal significance. Some of the species, notably *Galeolaria*, *Pyura* and the mussels, are of even greater importance since they furnish an important habitat for other smaller species. Thus any major alteration in the numbers of these belt forming species will have an important effect on the shore as a whole. Not only may the zonation be changed but, if one of the habitat forming species is removed, the whole species composition of the shore may be drastically altered.

One of the features of the shores of southern Australia is the relative poverty of the fauna and flora of the upper parts of the tidal region, and that any changes in zonation thus will be noticed. The changes noted above were all observed on coasts which experienced a low tidal range of less than 5' amplitude. Within such a narrow inter-tidal region any alteration in the belts is liable to be proportionately greater and liable to be noticed more easily than on a coast having a tidal range of 9' or more. The absence of large growths of algae makes the observation of such changes easier.

The fact that the changes in the belts occur amongst those organisms which are found at or near Mean Sea Level (M.S.L.) may be significant. It was calculated (Guiler, 1950) that *Galeolaria* occurs at about M.S.L. and suffers from 18.71% air exposure. *Hormosira* and *Mytilus*, occurring lower on the shore than *Galeolaria*, would have a somewhat less exposure, with a maximum of 26% for *Mytilus*. In my 1950 paper, working on a semi exposed coast, I suggested that there exists a lethal level at about M.S.L. at which a large number of species "cut out." It was also noted that the level of M.S.L. varies from month to month. This variation is only slight, but it may be sufficient to furnish a very varying and critical habitat to those species that dwell at or near that level. This is shown by the fact that a number of zone forming and other species cut out at about that level.

The evidence provided by the Coles Bay observation points to there being intense interspecific competition at least between certain species at this level, namely *Hormosira* and *Galeolaria*, *Hormosira* and *Mytilus*, *Austromytilus* and *Hormosira*, while the Dodge's Ferry evidence shows that *Galeolaria* and *Pyura* and *Mytilus* are in a state of constant interspecific

pressure, the absence of *Mytilus* enabling *Galeolaria* and *Pyura* to extend their vertical ranges. The limpet *Cellana* is dependent upon a smooth rock surface of sufficient area to permit the growth of algae and subsequent grazing by the limpet. Any encroachment upon their habitat by *Galeolaria* or barnacles will result in a restriction of the range of the limpet, and this is what happened at Blackman's Bay.

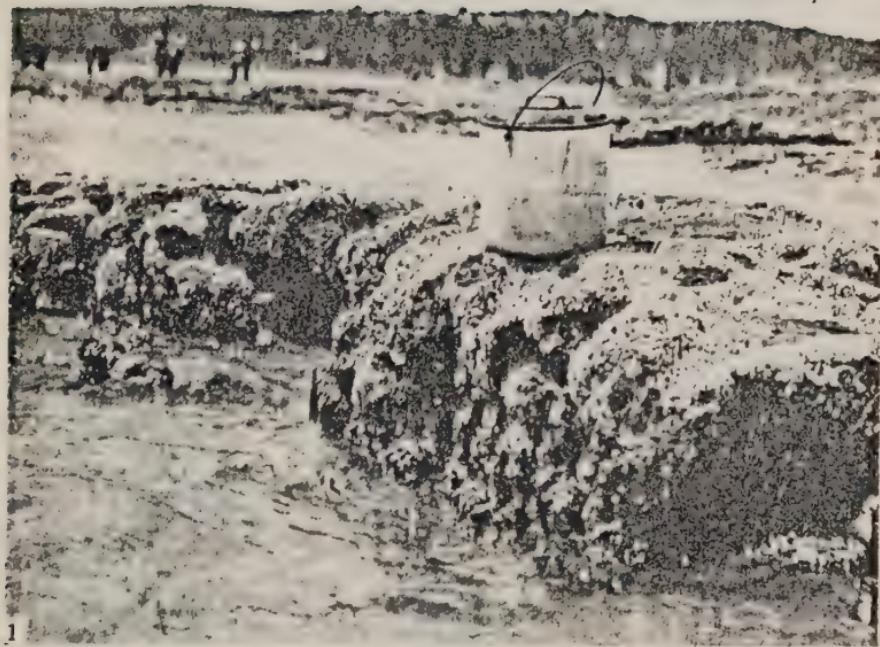
Southward and Crisp (1954) noted changes in the populations of British barnacles ascribing these changes to interspecific competition combined perhaps with other causes. Endean, Kenny and Stephenson (1956) record several instances where the zonation of the Queensland shores is controlled by interspecific competition. They found that *Pyura* overgrows *Galeolaria*, and that *Galeolaria* determines the lower limit of the barnacle zone.

Although interspecific competition is of great importance in determining the zonation, the conditions may be tipped in favour of one species or another by certain undetermined causes, as noted by Southward and Crisp. One feature of these changes is that only one species is immediately affected by them.

The thick masses of *Galeolaria* form in certain usually sheltered localities, and these aggregations apparently broke away from the substratum during the same year at widely scattered places on the Tasmanian coast, e.g., at Coles Bay, near the north-east, and Dodge's Ferry, in the south-east of the State. It may have been coincidence that this occurred at about the same time, but on the other hand it may well be part of a long-term cyclic change. It certainly was not due to a gale or gales. The immediate reason for the breakdown of the masses may be a mechanical breakdown of the tubes holding the mass to the substratum due to the excessive weight of the whole structure. This explanation may well be true of one group of *Galeolaria* tubes, but it can hardly suffice for hundreds of clusters breaking down at about the same time over at least 200 miles of coast. We can postulate a cycle or rhythm in *Galeolaria* with an initial high rate of larval settlement giving uniformly growing masses of *Galeolaria* tubes leading to tube clusters reaching a state of mechanical instability at the same time. All of the individual tubes in a *Galeolaria* aggregation are not of the same size, due to the settlement of subsequent larvae, but if this settlement rate is more or less the same over the whole coast then the breakdown will occur at the same time. This uniform rate of larval settlement is very difficult to concede, and at present I feel more inclined to ascribe the changes in *Galeolaria* population to some event or series of events, which may turn out to be cyclic in nature.

In the case of *Galeolaria*, some cause or causes led to the removal of the worm tubes from the rocks, and this created a biological vacuum on the shore. The surrounding unaffected organisms responded to this by a movement into the vacant area, as was also seen when *Mytilus planulatus* left a space on the shore at Dodge's Ferry. The rate of filling of the vacuum is not rapid, both where *Pyura* and *Mytilus* are the encroaching organisms.

However, the rate of recolonization by the zone forming species which had been removed may be very rapid. Experiments carried out on *Mytilus planulatus* beds at Blackman's Bay showed a very slow encroachment rate, but on removal of the whole mussel bed by a storm, the



1



2



Plate 2.

Fig. 1. *Galcolaria* masses at Dodge's Ferry, December, 1949. The shore was thickly coated with masses such as this.

Fig. 2. The shore at Dodge's Ferry, March, 1956. Note the absence of *Galcolaria* masses and mussel beds. *Pyura* (dark masses on the seaward edge of the rocks) has spread and become a dominant species.

pattern of zonation. Their conclusion can be applied to the coasts of Tasmania, where none of the alterations so far observed have done any more than slightly alter the zonation.

One important fact which has emerged from this long term project is that a collecting list made on one occasion may differ very greatly in its details from that made subsequently.

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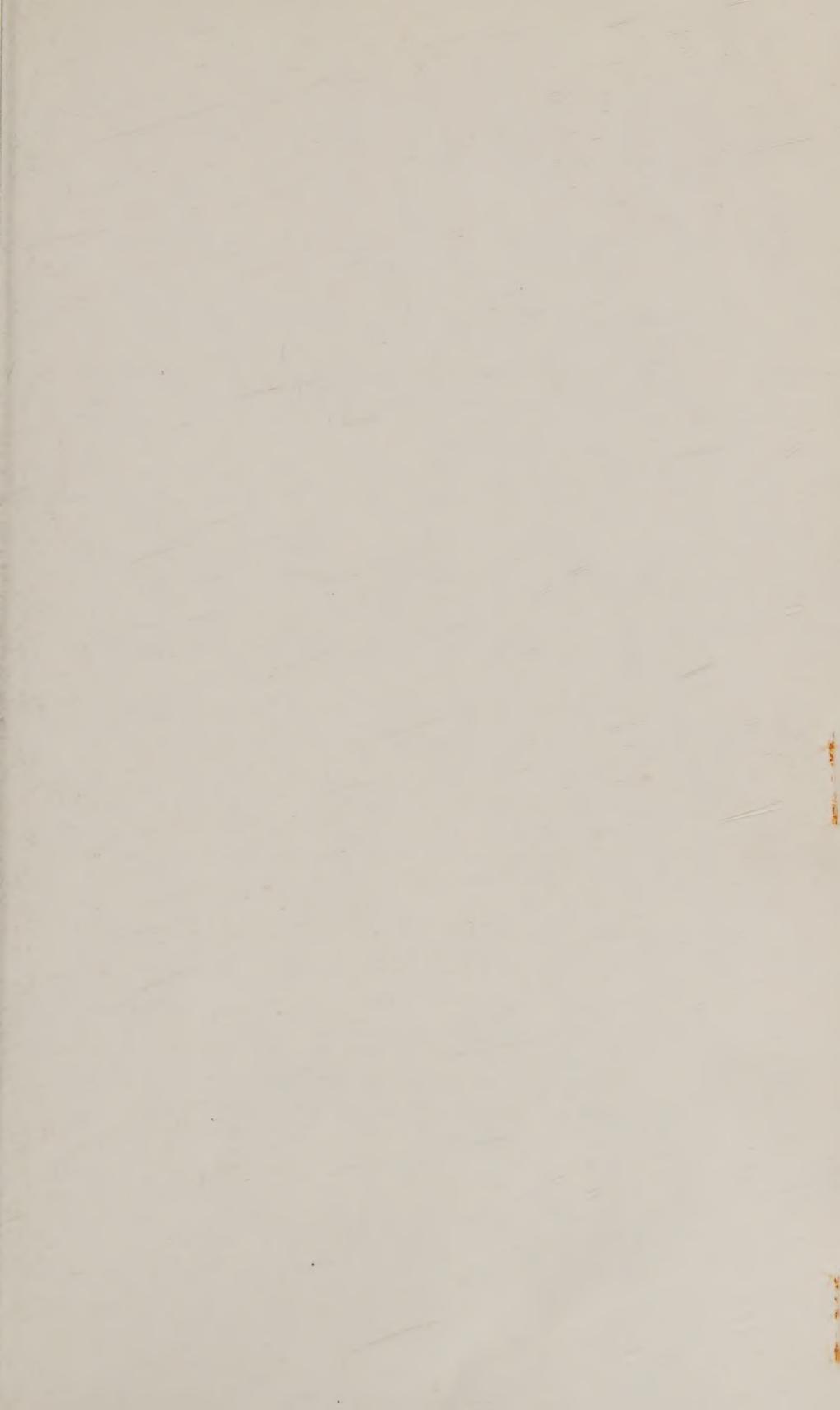
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